REGENERATION OF SOME FOREST AND GULLY COMMUNITIES IN THE ANGAHOOK–LORNE STATE PARK (NORTH-EASTERN OTWAY RANGES) 1–10 YEARS AFTER THE WILDFIRE OF FEBRUARY 1983

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Forest communities in the Angahook–Lorne State Park near Aireys Inlet include dry sclerophyll open-forest dominated by 18 m tall *Eucalyptus tricarpa* and various gully complexes. The number of plant species per community ranges from 43–130 and reflects differences in moisture, soils and topography.

Following the wildfire of February 1983, 77% of all species of vascular plants present before the fire reappeared within the first year and 98% (all but two species) returned within three years. The two species which did not reappear by year 3 (*Amyema pendulum* and *Hymenophyllum cupressiforme*) had still not returned by year 10.

Maximum post-fire species richness of vascular plants occurred in the early years after fire, then decreased by year 10 as vascular plant cover increased. In contrast, maximum post-fire species richness of non-vascular plants occurred 10 years after fire as canopy and understorey cover increased. Extensive carpets of two minerotrophic bryophytes (*Marchantia berteroana* and *Funaria hygrometrica*) and the fungus *Gerronema postii* appeared in damper areas of all communities during the first year after fire, and were not seen after year 3.

Approximately 62% of all vascular species which appeared in the first 3 years after fire, and still remained at year 10, had the capacity to regenerate vegetatively (or both vegetatively and from seed). The other 38% of vascular species regenerated from seed only.

The canopy in all communities recovered between 3 and 10 years reaching approximate pre-fire height and cover levels. Rate of recovery was faster in gully complexes than in drier *E. tricarpa* open-forest.

Seventy per cent of all species flowered or produced spores by the end of the third year. Twenty-five per cent of all species of trees and shrubs had not flowered or set seed by year 3, but did so by year 10.

Floristic and structural changes were seen in *E. tricarpa* open-forest where the previously open grassy understorey of *Poa sieberiana* (0.2 m tall) was replaced by a dense (4.0 m tall) understorey of fire induced or 'hard-seeded' shrubs including *Acacia verticillata*, *Goodenia ovata* and *Pultenaea daphnoides*.

Major floristic and structural changes also occurred in a gully complex where a peat fire was ignited by the wildfire and burnt to a depth of over 2 m for 3.5 months after the wildfire. Here the *Eucalyptus obliqua/Cyathea australis/Prostanthera lasianthos* complex was completely killed and replaced by seedling eucalypts which, by 10 years post-fire, formed a dense canopy (18 m tall) with no discernible understorey.

ON 17 February 1983 (Ash Wednesday) a wildfire burnt approximately 40 000 hectares of vegetation near Anglesea and Aireys Inlet, in the north-eastern Otway Ranges, Victoria (Rawson et al. 1983). Prior to 1983 there had been no published study on the fire ecology of the flora of this area. Following the wildfires, a ten year study of the post-fire recovery of vegetation and fauna was initiated (Reilly 1985, 1991a, 1991b; Wilson & Moloney 1985a, 1985b; Andersen 1987; Wark et al. 1987; Wark 1996).

The aims of the botanical study were to describe vegetation regeneration following wildfire in six of the major plant communities in the district (coastal heath, heath woodland, open-forest, sand-dune scrub, swamp thicket and gully complexes), and to provide information for use in the planning of conservation management. Regeneration of the heath and heath woodland communities in the first 10 years after fire has already been described (Wark et al. 1987; Wark 1996).

This paper presents data on regeneration of

Site	Location Height above SL Topography Geological origin	Fire history before Ash Wed.	Fire intensity Ash Wed. (Feb. 1983)	Subsite	Aspect	Soil type (A Horizon) 3 years after fire	Vegetation formation	Dominant species	Approx.** prefire height (m)	Height 3 years after fire (m)	No. of quadrats Yr 1, Yr 3	Area sampled (ha)
E (Bambra Road, Angahook -Lorne State Park)	2 km inland, 50-150 m above SL in watershed of Painkalac Creek. Topography hilly. Soils derived from Tertiary Eastern View Formation	Control burn approx. 1940. Bushfire 1962.	All Crown fired	E1	N/NE 11°	27 cm sandy clay loam, over sandy clay	Open Forest	*Eucalyptus tricarpa**	18.2	14.6	12, 12	2.0
				E2	S/SW 12°	32 cm sandy loam	Open Forest	*Eucalyptus tricarpa*, *Eucalyptus cypellocarpa* *Eucalyptus aromaphloia* and others	17.2	13.9	15, 15	2.0
				E3	N/NE 11° (bottom of gully leading to Ironbark Gorge)	ND[#]	Gully Complex	*Eucalyptus cypellocarpa* *Pomaderris aspera*	36.0	32.0	3, 3	0.1
F (near Distillery Creek Road, Angahook -Lorne State Park)	4 km inland, 50 m above SL in watershed of Distillery Creek. Topography hilly. Communities sampled were at bottom of gully. Soils derived from Tertiary Eastern View Formation	No fire for approx. 100 years	Crown fired	F1	N 0° (bottom of gully beside Distillery Creek)	>90 cm peaty loam	Gully Complex	*Eucalyptus obliqua* *Cyathea australis* *Prostanthera lasianthos*	14.0	14.0	5, 5	0.1
			Crown fired, then peat fire	F2	N 0° (bottom of gully)	>90 cm burnt peat	Modified Gully Complex	*Eucalyptus obliqua* *Eucalyptus willisii*	14.0	5.0	2, 5	0.1

Table 1. Site descriptions of forest and gully communities. *Modified by human interference. **Tallest stratum. [#]ND=not done.

E. tricarpa open-forest and various gully complexes ten years after the 1983 fire and describes their floristics and structure. Regeneration strategies and post-fire flowering response of species are also described. Mammal, bird and insect data have been studied and reported separately (Reilly 1985, 1991a, 1991b; Wilson & Moloney 1985a, 1985b; Andersen 1987).

SITE DESCRIPTIONS

Two sites (E and F) which supported native vegetation, and which were relatively undisturbed by European man (Fig. 1, Table 1), were selected in undulating terrain on soils derived from Tertiary sediments known as the Eastern View Formation (Pitt 1977, 1981). The sites were located 2.5–4.0 km inland from the coast, in the Angahook–Lorne State Park, near Aireys Inlet. Each contained one or more plant communities (subsites), including *Eucalyptus tricarpa* (red Ironbark) open-forest (subsite E1), *E. tricarpa* mixed open-forest (subsite E2), and various gully complexes (subsites E3, F1 and F2). The term open-forest follows Specht (1970), the term 'gully complex' is used because these small riparian communities were very narrow, disjunct and uncommon, and contained varied proportions of broad leaf and sclerophyll vegetation.

Subsite E1 was on a north-facing slope. Here the overstorey was an almost pure stand of *E. tricarpa*, generally of a similar age and density. On the adjacent southerly slope (subsite E2) the overstorey eucalypts were of mixed age, density and species and included *E. tricarpa*, *Eucalyptus cypellocarpa*, *Eucalyptus aromaphloia* and others. Both subsites E1 and E2 had light grassy understoreys before the fire (Parsons et al. 1977).

Both sites had been affected by timber cutting between 1860 and 1920, and were controlled by the Forests Commission of Victoria between 1921 and 1987. During this second period, understorey reduction and thinning was carried out from time to time, as part of local fire-prevention strategies (P. Denham, pers. comm.). It is not known whether subsites E1 and E2 were affected by these practices.

The gully complexes studied were discontinuous, often occurring in narrow bands (max. width 20–50 m) beside semi-permanent streams. All were surrounded by dry sclerophyll open-forest with a eucalypt overstorey. The complex adjacent to the creek running through Ironbark Gorge (subsite E3) occurred on silty soil, and those adjacent to Distillery Creek (subsites F1 and F2) on peaty soil and (after Feb. 1983) burnt peat soil respectively. Overstorey species in these included *Eucalyptus cypellocarpa* and *Eucalyptus obliqua*, varying proportions of the broad-leafed understorey shrubs *Pomaderris aspera* and *Prostanthera lasianthos* and the ferns *Cyathea australis* and *Todea barbara*.

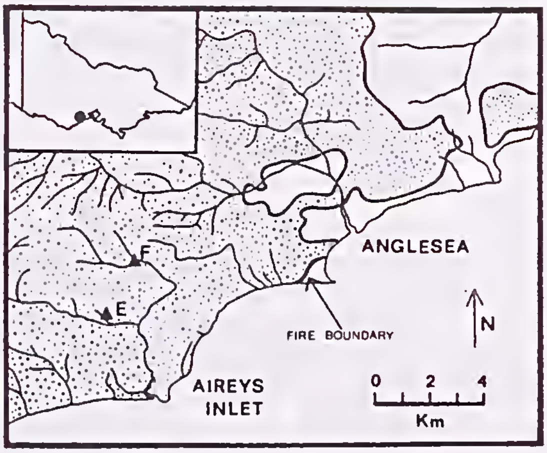


Fig. 1. Locality map showing location of the eastern Otway Ranges, Victoria and sites E and F near Anglesea. Stippling indicates the area burnt on 17 February 1983. The fire advanced from the south west.

The previous fire history of each site differed (Table 1). The high-intensity wildfire of February 1983 destroyed all ground strata vegetation and crown-fired the eucalypt overstorey at all subsites (Table 1). The fire occurred following a drought in 1982, which intensified in January, February and March 1983 (in 1982 the total annual rainfall of Anglesea was 452 mm compared with the annual mean of 657 mm). Over 80 mm of rain fell one month after the fire and then at 3, 7 and 8 months post-fire causing soil erosion and hill wash at subsites E1, E2 and E3, and often removing the top 2–4 cm of humus and ash-rich soil of the upper A horizon. Total rainfalls for 1983–1993 were about or above average except for years 1986, 1988, 1990 and 1991, when they were 622, 643, 596 and 614 mm respectively (Wark et al. 1987; Wark 1996).

A peat fire, started by the wildfire, established at subsite F2 and gradually burnt the soil in half the gully to a depth of about 2.0 m. It was finally extinguished by early winter rains in June 1983. In the area where this peat fire burnt for 3 months, the ground sank, the creek bank collapsed, and large areas of burnt peat were washed away.

Because of the extent of the Ash Wednesday fires, no unburnt sites comparable with sites E and F were available for study.

METHODS

Soils

Soil profile data. Methods of soil description and analysis follow Wark et al. (1987). Surface (0–10 cm) soil samples collected at 2 months and 1 and 2 years after fire were analysed for pH, available P, total Kjeldahl N, organic C, and exchangeable Na, K, Ca and Mg by the State Chemistry Laboratory, Victoria. The A horizon profile was examined at 3 years (by Dr D J Robertson, Wark et al. 1987) by digging pits down to the upper B2 horizon, and recording colour, texture and depth.

Pot experiments. A bioassay was carried out to assess fertility of black unburnt peat soil from F1 and red burnt soil from F2 using samples collected two years after the wildfire. Seed of *Eucalyptus obliqua* was collected adjacent to subsites F1 and F2. *E. obliqua* seedlings were grown at Aireys Inlet for 8 months on the two soils (1 seedling/ 75 mm diameter pot, 15 pots/treatment) in a shade house from autumn to spring. Shoot height of each group was measured monthly for 8 months, and mean growth rates determined. After 8 months, dry weight of roots and shoots and root/shoot ratios were determined.

Vegetation

Pre-fire data. Detailed species lists of vascular plants existed for each site prior to the 1983 fire (White 1982). However, no quantitative data on pre-fire floristics or vegetation structure were available. Approximate pre-fire height was interpreted from pre-fire photographs and the height of burnt tips. Approximate pre-fire projective cover was also estimated from pre-fire field observations and photographs.

Data collection. Forty 1×3 m permanent quadrats (Table 1) surrounded by permanent extended plots (11×13 m) were used for data collection at 2, 6 and 10 months and in spring 1, 3, 7 and 10 years after fire. At site E, quadrats were in groups of three 20 m apart set at 90 m intervals along transect lines 300–350 m long. At subsite F1, quadrats were placed in a Maltese cross, and at subsite F2 they were distributed randomly.

Methods used to collect and analyse floristic and structural data (including canopy regrowth) and determine flowering and regeneration response have been previously described (Wark et al. 1987; Wark 1996).

Total species lists were made for each subsite at each survey, and these used to supplement quadrat data on floristics, flowering and regeneration strategies. As in Wark et al. 1987 and Wark 1996, the term 'total number of species' at a site (or subsite) refers to the total number of species recorded in the quadrats plus any additional species recorded at the site (or subsite). In the present paper, quadrat data alone are used to analyse the relationship between plant species richness and total vascular plant cover.

Girth of trunks of the overstorey and understorey were measured at 1.45 m (girth at breast height, GBH). Data on the eucalypt overstorey in open-forest was derived from measurements of a minimum of 20 trees of the tallest stratum. In this paper, the term understorey (or shrub stratum) will include the ground stratum; the term herb will be used to mean an herbaceous species; and the term graminoid will not be used.

Nomenclature of vascular plants follows Ross (1996); for Orchidaceae—Backhouse & Jeanes (1995); mosses—Scott & Stone (1976); liverworts—Scott (1985); and lichens—Filson & Rogers (1976). Introduced species were identified by the National Herbarium of Victoria.

The species described as *Marchantia polymorpha* in Wark et al. 1987 was incorrectly identified. It was in fact *Marchantia berteroana* Lehm. & Lindenb. (Scott 1985). Similarly, the fungus *Omphalia chromacea* is now known to be *Gerronema postii* (Fr.) Singer (May & Fuhrer 1989); and the herb *Viola hederacea* ssp. *sieberiana* now known to be *Viola cleistogamoides*. Name changes of vascular plants which have occurred since the first paper in this series (Wark et al. 1987) are given in Wark 1996 and in the Appendix of the present paper.

Regeneration strategies terminology follows Purdie (1977a, 1977b), namely: OSR=obligate seed regenerator (regenerating from seed or propagules only); FRR=facultative regrowth regenerator (regenerating by regrowth, and from seed or propagules); ORR=obligate regrowth regenerator (regenerating by regrowth only).

RESULTS

Soils

Profiles. Soil profile data are given in Table 2. At E1 and E2, hill wash and soil erosion occurred one month after the fire, and in places the top

Community (subsite)	Year after fire	pH (H_2O)	Exch. Na c mol(+)/kg	Exch. K c mol(+)/kg	Exch. Ca c mol(+)/kg	Exch. Mg c mol(+)/kg	Avail. P mg/kg	Total Kjeldahl N g/g^{-2}	Organic C g/g^{-2}	C/N
Open forest (E1)	1*	5.8	0.50	0.28	0.98	2.09	2.0	0.11	3.2	25.0
	2**	5.7	0.45	0.23	0.80	1.34	1.3	0.13	3.3	31.0
Open forest (E2)	1	5.3	0.22	0.23	0.48	0.48	1.6	0.10	2.2	24.0
	2	5.5	0.33	0.23	0.77	0.58	1.4	0.11	2.7	15.0
Gully complex (F1)	1	5.1	0.30	0.60	0.10	1.60	3.5	0.49	9.3	19.0
	2	5.5	0.57	1.10	0.60	4.18	1.7	0.60	12.1	20.0
Modified gully complex (F2) (burnt peat)	1	5.5	0.20	0.60	1.30	1.28	11.4	0.30	2.1	7.0
	2	6.0	<0.09	0.80	0.50	1.28	3.6	0.21	3.2	15.0

Table 2. Soil analysis of the A horizon (0–10 cm) of forest communities 1 and 2 years after fire. *Year 1 values are from single samples. **Year 2 values are from composite samples of 40 cores.

0–6 cm of the humus-rich and ash-rich A1 horizon was removed exposing a compacted A2 horizon of 6–32 cm. Cracking of this layer was common and patches of hydrophobic soil were observed.

The soil at subsite F1 was a black peaty loam >0.9 m in depth. Burning of this peaty loam (subsite F2) produced a friable material 0.9 m–2.0 m deep. In this paper, this material will be called 'burnt peat'. The colour of this burnt peat was in the Munsell 'red' Range. During the 3 years following the fire, a brown 5 cm litter layer developed on the top of the burnt peat. The burnt peat gradually sank 0.5–1.0 m in the years following the fire and erosion channels up to 1.5 m deep developed near the creek.

Chemical analyses. Topsoil samples taken at the subsites 1 and 2 years post-fire ranged in pH from 5.1–6.0 (Table 2). Subsites E1 and E2 were both low in nutrient cations and organic matter. The soil at subsite F1 was higher in organic matter and N than subsite F2. The soil at subsite F2 was high in available P, 1 year after the fire. Soils of both subsite F1 and F2 retained high levels of exchangeable K between years 1 and 2.

Analyses of 1 and 2 year post-fire topsoil samples showed no significant change in nutrient levels between these times (Table 2, $P>0.05$, t test), and suggests that any 'ash bed' effect had disappeared by the first year. Unfortunately topsoil samples collected two months after the fire were mislaid.

Pot growth experiments with E. obliqua. Growth of *E. obliqua* was faster on peat soil derived from subsite F1 ($P>0.05$, t test) than from F2. Seedlings on the burnt peat grew rapidly initially then slowed in growth and became chlorotic. Seedlings planted on unburnt peat grew steadily and appeared normal compared with those on burnt peat. Mean root/shoot ratios at the end of the experiment were 0.39 and 0.61 (for subsites F1 and F2 respectively).

Throughout the experiment, levels of available P remained high in burnt (cf. unburnt) soil.

Vegetation

Floristics. The floristics of the plant subcommunities one, three and ten years post-fire are presented as presence–absence data in Table 3.

(a) Number of species. A total of 182 species of vascular plants was recorded prior to the fire (Table 3). With the exception of 2 species, all reappeared in the first 3 years after fire. The mistletoe *Amyema pendulum* and the filmy-fern *Hymenophyllum cupressiforme* (which were present before the fire) did not reappear in the 10 years following the fire. A total of 44 species of non-vascular plants (liverworts, mosses and lichens) appeared sequentially during the 10 years after fire.

A total of 9 tree species, 40 shrubs, 116 species of herbs (including 20 orchid species), 7 creepers and climbers, 8 ferns and 44 species of non-vascular plants were present post-fire (Table 3).

(b) Diversity of plant communities. Plant communities were floristically diverse (Table 3). Species numbers 10 years post-fire ranged from 120–130 for open-forest subcommunities, 76–82 for gully complexes, and 43 for the modified gully complex. Forty to seventy per cent of species in each sub-community were sampled in the 1×3 m permanent quadrats at year 3, giving a species richness in quadrats of 22–48 species. Nine species were found in all 5 subcommunities, including *Acacia verticillata*, *E. cypellocarpa*, *Goodenia ovata*, *Tetrarrhena juncea*, *Gahnia radula* and several species of herbs and nonvascular plants. Floristics of these subcommunities are presented as presence-absence data in Table 3.

Computer analysis of combined year 1 and year 3 data (by Dr D. J. Robertson, Charles Sturt University; see Wark et al. 1987), using both classification and ordination techniques (data not presented here), confirmed the presence of at least 5 distinct subcommunities (all with shrubby understoreys—subsites E1, E2, E3, F1 and F2, Table 3) and identified floristic differences between them. Ordination results confirmed the classification data.

Floristic differences and stature of dominants between open-forest and gully complexes appeared to reflect variations in drainage, soils and topography. Open-forest occurred on sloping sites with sheet-eroded silty-clay soils, whereas gully complexes occurred beside creeks, on silty or peaty soils.

(c) Changes in species richness with time. Maximum post-fire species richness occurred in the early years after fire (Table 3, Fig. 2).

In both forest and gully communities, the species richness of vascular plants in quadrats decreased (Figs 2A, 2C) as vascular plant cover increased (Figs 2B, 2D). In contrast, in forest and gully communities the species richness of non-vascular plants either increased or increased then plateaued (Figs 2A, 2C) as vascular plant cover increased (Figs 2B, 2D).

Subsite Vegetation formation	E1 Open forest	E2 Open forest	E3 Gully complex	F1 Gully complex	F2 Modified gully complex
Trees **					
Myrtaceae					
Eucalyptus aromaphloia		(1) (3) (10)			
Eucalyptus baxteri				1 3 10	(3)
Eucalyptus cypellocarpa	1 3 10	1 3 10	1 3 10	1 3	1 (3)
Eucalyptus globulus ssp. *bicostata*		(1) (3) (10)			
Eucalyptus obliqua		1 3 10		1 3 10	1 3 10
Eucalyptus ovata					1
Eucalyptus tricarpa	1 3 10	1 3 10	(1) (3) (10)		
Eucalyptus viminalis				(1) (3)	
Eucalyptus willisii	(1) (3) (10)	1 (3)		1 3	1 3 10
Eucalyptus (spp.)	1 10	1 3 10	1	1	1
Tall shrubs †					
Labiatae					
Prostanthera lasianthos			1 3 10	1 3 10	(10)
Mimosaceae					
Acacia dealbata	(1) (3)		(10)		
Acacia mearnsii	(1) (3) (10)				
Acacia melanoxylon	(1) (3) (10)				
Acacia pycnantha	(1) (3) (10)	(1) (3) (10)			
Acacia spp.			(10)		
Santalaceae					
Exocarpos cupressiformis	1 (3)	(1) 3			
Shrubs †					
Asteraceae					
Olearia argophylla			(1) (3) (10)		
Olearia lirata				(3) (10)	
Olearia phlogopappa	1 3 10	(1) (3) (10)	1 3 10	(1) (3) (10)	
Olearia ramulosa	(1) (3)				
Olearia teretifolia	(1) 3 (10)				
Ozothamnus ferrugineus		(10)	(10)	(3) (10)	
Dilleniaceae					
Hibbertia riparia		(1) (3) (10)			
Epacridaceae					
Acrotriche serrulata		(1) 3 10			
Astroloma humifusum	(1) (3) (10)	(1) (3) (10)			
Epacris impressa	(1) 3 10	1 3 10	1 3 10		
Lissanthe strigosa	(1) (3)				
Goodeniaceae					
Goodenia ovata	1 3 10	1 3 10	1 3 10	1 3 (10)	1 3
Fabaceae					
Indigofera australis			(1) (3) 10		
Pultenaea daphnoides	1 3 10	1 3 10		1 (3)	
Pultenaea scabra	(1) (3) (10)				
Loranthaceae					
Amyema pendulum ¥					
Mimosaceae					
Acacia acinacea	(1) (3)				
Acacia genistifolia	(1) (3) (10)	(1) (3)			
Acacia mucronata	(1) (3) (10)				
Acacia myrtifolia	(1) (3) (10)	(1) (3)			

Table 3 continued next page (see legend on page 19)

Subsite Vegetation formation	E1 Open forest	E2 Open forest	E3 Gully complex	F1 Gully complex	F2 Modified gully complex
Acacia verniciflua	1 3 10	1 3 10	(1) (3) (10)		
Acacia verticillata	1 3 10	1 3 10	1 3 10	1 3 10	1 3 10
Acacia spp.	(1)	(1)	(1) (10)	1	
Myrtaceae					
Leptospermum continentale			(10)	1 (3) (10)	(3)
Meloleuca squarrosa				(1) (3) (10)	
Pittosporaceae					
Bursaria spinosa		(1) (3) (10)	(10)		
Proteaceae					
Lomotia ilicifolia		(1) (3) (10)			
Rhamnaceae					
Pomaderris aspera			1 3 10	3 (10)	
Pomaderris ferruginea	(1) 3 10			(3) (10)	
Pomaderris elachophylla				3 (10)	(3)(10)
Spyridium porvifolium	(10)	1 10	1 3 10	1 3 10	10
Rubiaceae					
Coprosma quadrifida			(1) (3) (10)		
Rutaceae					
Correa reflexa			(1) 3 10		
Solanaceae					
Solanum laciniatum	(1) (3)				
Thymelaeaceae					
Pimelea humilis	(1) (3) (10)	(1) (3)			
Pimelea linifolia	(3)				
Lichens†					
Cladia aggregata	(3) 10	10		10	
Cladonia cervicormis ssp. *verticillata*	10				
Cladonia chlorophaea	10				
" *corniculata*	10				
" *ramulosa*	10				
" *scabriusula*	10				
" *tessellata*	10				
" spp.	10	10			(10)
Psoroma sp.					10
Thyanothecium scutellatum	10	10			
Usnea sp.? *confusa*	10				
" ? *inermis*	10				
Unidentified spp.	1 (3)	1		(3)	(3)
Liverworts†					
Asterella drummondii			(3)	3	3
Anthoceros laevis			3	3	
Cephaloziella exiliflora		10		3 10	3
Lethocolea pansa		3	3		
Lophocolea semiteres		10		3 10	3 10
Marchantia polymorpha	1	1	1 3	1 3	1 3
Symphogyna podophylla				3	
Unidentified spp.				3	3
Chaetophyllopsis whiteleggei		(10)			

Table 3 continued next page (see legend on page 19)

Subsite Vegetation formation	E1 Open forest	E2 Open forest	E3 Gully complex	F1 Gully complex	F2 Modified gully complex
Lepidozia laevifolia		10			
Lophocolea muricata					10
Metzgeria decipiens				10	
Riccardia aequicellularis	10	10	10		
Fungi †					
Gerronema postii	(1)	(1)	(1)	(1) 3	
Unidentified spp.	(3) (10)	(3) (10)	(3) (10)	(1) (3) (10)	(1) (3)(10)
Mosses†					
Barbula calycina	3 10	3 10	3		
Breutelia affinis	10			3	
Bryum billardieri		3		3 10	3 10
Bryum campylothecium	10	10			
Bryum capillare	(10)				
Bryum pachytheca	3	3			
Bryum sp.		10			
Campylopus australis	(10)	10			
Campylopus introflexus	3 10	3 10	3	3 10	(10)
Campylopus pyriformis		10		3	
Campylopus sp. nova		10			10
Ceratodon purpureus	3	3	3	3	3
Fissidens tenellus		10			
Funaria hygrometrica	1 3	1 3	1 3	1 3	1 3
Hypnum cupressiforme				10	
Polytrichum juniperinum	3 10	3	3	3	3 10
Ptychomnion aciculare		10		10	10
Sematophyllum amoenum		10	(10)	10	10
Tayloria octoblepharis		10			
Wijkia extenuata		10			10
Unidentified spp.	1 3	1 3	1 3		
Ferns & Allies †					
Adiantum aethiopicum			(1) (3) (10)		
Blechnum cartilagineum			1 3 (10)		
Blechnum nudum				1 3 10	
Cyathea australis			(1) (3) (10)	1 3 10	10
Gleichenia microphylla				(3) (10)	
Hymenophyllum cupressiforme ¥¥					
Hypolepis rugosula			(3) (10)		3 (10)
Pteridium esculentum		1 3 10	1 3 10	1 3 10	1 3 10
Todea barbara				1 3 10	
Unidentified (young) spp.				3 (10)	
Sedges & Rushes †					
Cyperaceae					
Gahnia radula	1 3 10	1 3		10	
Gahnia sieberiana			(1) (3) (10)	1 3 10	(3)
**Isolepis hystrix*				1	
Isolepis inundata				1	
**Isolepis marginata*	1	1	1	1 3	
Lepidosperma elatius			(10)	1 3 10	1 3 (10)
Schoenus apogon			3	1	

Table 3 continued next page (see legend on page 19)

Subsite Vegetation formation	E1 Open forest	E2 Open forest	E3 Gully complex	F1 Gully complex	F2 Modified gully complex
Juncaceae					
Juncus pauciflorus				3	3
Juncus planifolius				1	
Luzula meridionalis			3		
Grasses†					
Gramineae					
Agrostis avenacea		1			
**Aira caryophyllea*	3	1 3	3		
**Anthoxanthum odoratum*		1			
Austrostipa semibarbata	(1) (3)				
Austrostipa rudis	(1)				
**Briza minor*			(3)		
Danthonia geniculata	(1)				
Danthonia induta	1	(1)			
Danthonia pilosa	(1)				
Danthonia procera	(1)				
Danthonia setacea	(1)				
Danthonia spp.		(10)			
Deyeuxia densa		3	3	1	
Deyeuxia quadriseta		1	1		
Dichelachne rara	1 3	1 3	3		
Echinopogon ovatus	(1)				
**Holcus lanatus*	(1)				
Joycea pallida		(1)			
Microlaena stipoides	1	1	1		
Notodanthonia semiannularis	(1)				
Poa morrisii		10 (1)			
Poa sieberiana	1 3 10	1 3 10	1 3		
Poa tenera				(10) 1 3	10
Tetrarrhena distichophylla	1 3 10				
Tetrarrhena juncea	3 10	1 3 10	1 3 10	1 3 10	1 3 10
**Vulpia myuros*	(1) (3)				
Unidentified grasses	1 3 10	3 10	3 (10)	1	
Orchids†					
Orchidaceae					
Acianthus caudatus	(3)				
Acianthus pusillus	1 (3) 10			(10)	
Caladenia cardiochila	(1) (10)				
" *catenata*	(3) (10)	(1) (3)			
" *tentaculata*	(3) (10)	(1)			
" *menziesii*	1	1 3			
" *reticulata*		(1) (3)			
Cyrtostylis reniformis		3			
Dipodium punctatum	(1) (3)	(1)			
Eriochilus cucullatus	(1) (3)				
Prasophyllum odoratum	10	1 (3)			
Pterostylis longifolia	(3) 10	(3) 10			
Pterostylis nutans	10		(1)		
Pterostylis nana	(3) 10		3		
Pterostylis parviflora		3			
Pterostylis sanguinea		(1)			

Table 3 continued next page (see legend on page 19)

Subsite Vegetation formation	E1 Open forest	E2 Open forest	E3 Gully complex	F1 Gully complex	F2 Modified gully complex
Thelymitra flexuosa	3				
Thelymitra ixioides	(3) 10				
Thelymitra pauciflora	(3) (10)				
Thelymitra rubra	(3)				
Thelymitra spp.	(1) (3)				
Lilies & Irises †					
Liliaceae					
Caesia parviflorus		(1) (3)			
Burchardia umbellata	3 10	1			
Dianella revoluta	(10)	1			
Lomandra filiformis	1 3 10	1 3 10			
" *longifolia*	10	1 3 (10)		3	
" *multiflora*		(1) (3)			
" *micrantha*		(1) (3) (10)			
Lomandra spp.	(1) 10	(1) 10			
Thysanotus juncifolius				1	
" *tuberosus*		1 3			
" *patersonii*	1 3 10				
Herbs †					
Asteraceae					
**Aster subulatus*			3	3	3 10
**Carduus tenuiflorus*				1	
**Cirsium vulgare*	(1) 3			1 (3)	
Euchiton involucratus		1 3 (10)	(1) (3)		
Euchiton sphaericus			(1)		
Ozothamnus ferrugineus				(3)	(3)
Helichrysum leucopsideum		(1)			
Helichrysum scorpioides	(1)				
**Hypochoeris radicata*	(1) (3) (10)				
Lagenifera gracilis	1 3 (10)				
Lagenifera stipitata	(1)				
Leptorhynchos linearis	(1)				
Leptorhynchos squamatus	(1)				
Senecio velleioides			(1) 3	1	
Senecio spp.					3
**Sonchus oleraceus*			3		
Boraginaceae					
Cynoglossum suaveolens	(1) (3)	(1) (3)			
Brunoniaceae					
Brunonia australis		1 3			
Campanulaceae					
Wahlenbergia gracilenta	(1) (3)	1 3	3	1	
Wahlenbergia stricta	(1) (3) (10)	(10)			
Caryophyllaceae					
Stellaria flaccida			1 3 10	1 3 10	1 3 10
Stellaria pungens		1 (10)			
**Stellaria media*		1			
Cruciferae					
Rorippa dictyosperma			1	1	
Droseraceae					
Drosera peltata ssp. *auriculata*	1 3 (10)	1 3 10			

Table 3 continued next page (see legend on page 19)

Subsite Vegetation formation	E1 Open forest	E2 Open forest	E3 Gully complex	F1 Gully complex	F2 Modified gully complex
Drosera peltata	1 3 (10)	1 3 10	(1) 3	3	
Drosera macrantha		(1) 10			
Drosera whittakeri		(1) (3)			
Euphorbiaceae					
Poranthera microphylla	(1)	(1)			
Phyllanthus gunnii				3	
Gentianaceae					
**Centaurium spicatum*	(1) (3) (10)			(10)	
Geraniaceae					
Geranium solanderi	1 3 (10)	1 3	1 3 10		
Pelargonium australe	1	1	1		
Geranium spp.		(1)	(1)		
Goodeniaceae					
Goodenia lanata	1 (3)	1 3 (10)			
Haloragaceae					
Gonocarpus tetragynus	1 3	1 10	1 3	1 3	1 3
Hypericaceae					
Hypericum gramineum	1 3 (10)				
Lobeliaceae					
Lobelia gibbosa	(1)	(1)			
Lobelia rhombifolia	(1)				
Oxalidaceae					
**Oxalis corniculata*	1 3 10		1 3 10	1 3 (10)	
Plantaginaceae					
Plantago varia	1 3	1 3 10	3		
Rosaceae					
Acaena novae-zelandiae		(1) (3)			
Rubiaceae					
Asperula scoparia	10		1	1 3 10	
Galium binifolium	1 3 (10)		(10)		
Opercularia varia	1 3 (10)	1 3	1 3	1	1
Scrophulariaceae					
Veronica calycina			1 3		
Veronica derwentiana			(1) 10		
Violaceae					
Viola hederacea	(1) 3 (10)	1 3 10	1 3 10	1 3 10	
Viola cleistogamoides				(1) 3 10	1 3
Convolvulaceae					
Dichondra repens	10	(3)			
Umbelliferae					
Hydrocotyle callicarpa	1	1	1 (10)		
Hydrocotyle hirta			1	1 3 10	
Hydrocotyle laxiflora	1	1			
Creepers & Climbers †					
Lauraceae					
Cassytha glabella	1 (3)	1 (3) (10)		1	1
Cassytha melantha	3	3			
Pittosporaceae					
Billardiera scandens	(1) 3 (10)	(1) 3 10	1 3 10	1 3 10	
Polygalaceae					
Comesperma volubile	3 (10)	(1) 3 10		(3)	
Ranunculaceae					
Clematis aristata		1 3 10	1		

Table 3 continued next page (see legend on page 19)

Subsite Vegetation formation	E1 Open forest	E2 Open forest	E3 Gully complex	F1 Gully complex	F2 Modified gully complex
Fabaceae					
Kennedia prostrata	1 3	1 3			
Glycine clandestina			1 3		
Seedlings					
Monocotyledon	1	1	1	1	1
Dicotyledon	1 10	1	1	1	1
Sub-total vascular species in quadrats Year 1, Year 3, Year 10	35, 34, 28	46, 36, 25	30, 33, 25	39, 34, 24	14, 14, 9
Sub-total additional vascular species at site Year 1, Year 3, Year 10	48, 39, 30	35, 26, 17	15, 12, 16	4, 10, 11	-, 6, 4
Total vascular species[δ] Year 1, Year 3, Year 10	83, 73, 58	81, 62, 42	45, 45, 41	43, 44, 35	14, 20, 13
Sub-total non-vascular species in quadrats Year 1, Year 3, Year 10	3, 6, 17	3, 8, 19	2, 8, 1	2, 14, 10	2, 8, 10
Sub-total additional non-vascular species at site Year 1, Year 3, Year 10	1, 2, 2	1, 2, 1	1, 1, 1	1, 3, -	2, 2, 1
Total non-vascular species[δ] Year 1, Year 3, Year 10	4, 8, 19	4, 10, 20	3, 9, 2	3, 17, 10	4, 10, 11
Total species[δ] Year 1, Year 3, Year 10	87, 81, 77	85, 72, 62	48, 34, 43	46, 61, 45	18, 30, 24
Total species[δ] Years 1-3 combined	106	100	62	74	32
Total species[δ] Years 1-10 combined	130	120	76	82	43
Total species[δ] Years 1-10 combined	224 species 180 species vascular plants 44 species non-vascular plants				

Table 3. Floristic comparisons between subsites 1, 3 and 10 years after fire. *Key:* 1=present in quadrats year 1; 3=present in quadrats year 3; 10=present in quadrats year 10; (1)=present at site year 1; (3)=present at site year 3; (10)=present at site year 10; *introduced species; **12×13 m quadrats; †1×3 m quadrats; δ=total species present in quadrats plus additional species present at site. ¥*Amyema pendulum*—present at subsites E1 and E2 before the fire in the eucalypt canopy at 15–20 m. Not recorded years 1–10 post-fire. ¥¥*Hymenophyllum cupressiforme*—present before the fire at subsite F1, growing on *Cyathea australis*. Not recorded years 1–10 post-fire.

Combining site and quadrat data, maximum post-fire species richness of vascular plants occurred during years 1–3, decreasing by year 10 to 54% of the years 1–3 level (180 species years 1–3 combined; 97 species year 10; Table 3). However, the species richness of non-vascular plants in years 1–3 combined was 50% that observed in year 10 (18 species years 1–3 combined; 35 species year 10; Table 3). Of the 44 species of non-vascular plants, 27 appeared between years 3 and 10 post-fire as canopy and understorey cover increased.

(d) Dominant species. The proportion of tree and shrub species was similar for both open-forest and gully complexes. However, open-forest contained more grass, lily, orchid and other herbaceous species than gully complexes, which contained more species of liverworts, ferns and sedges (Table 3).

Eucalyptus tricarpa was the dominant eucalypt

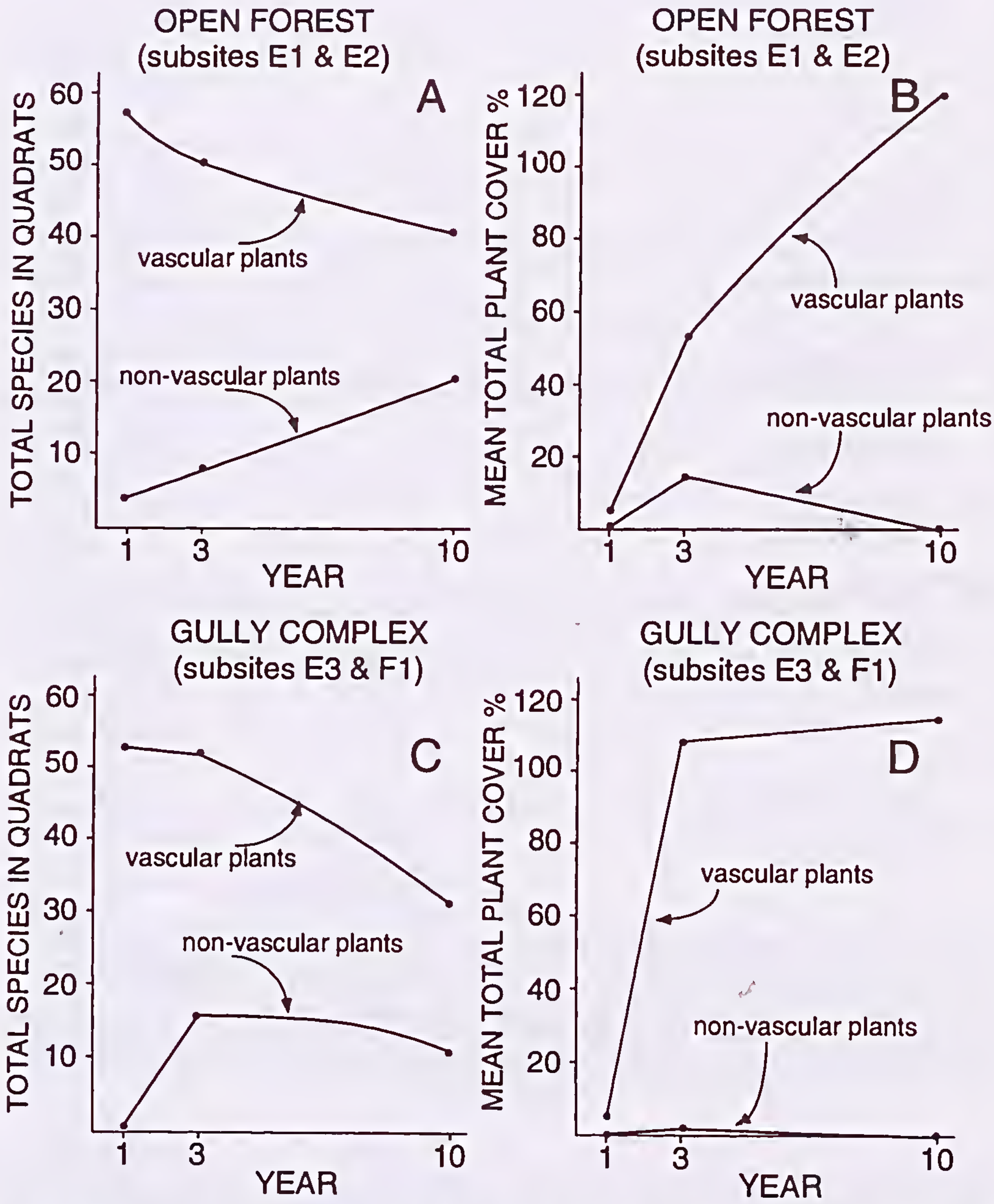


Fig. 2. Species richness and plant cover (%) at 1, 3 and 10 years post-fire. A, Species richness in open-forest (subsites E1 and E2 combined). B, Cover (%) in open-forest (subsites E1 and E2 combined). C, Species richness in gully complex (subsites E3 and F1 combined). D, Cover (%) in gully complex (subsites E3 and F1 combined).

of the open-forest communities (subsites E1 and E2). On the north facing slope (subsite E1—Fig. 3) it comprised 87% of all trees in the total population (690 stems/ha), and occurred as single-trunked trees mean 18.2 m tall (SD 2.82, range 14.6–22.8 m) of girth 97.4 cm (SD 20.2). On the south-facing slope (subsite E2) it comprised 80% of all trees in the total population (1000 stems/ha), again occurring as single-trunked trees mean 17.2 m tall (SD 3.4, range 12.4–22.6 m), of girth 108 cm (SD 42).

Gully complexes were dominated by *Eucalyptus cypellocarpa* at subsite E3, and *Eucalyptus obliqua* at subsite F with a density of 10–20 trees/ha (subsite F1—Fig. 4). The *E. cypellocarpa* at subsite E3 were large old single-trunked trees 30–35 m tall and of GBH >1.5 m. The *E. obliqua* at site F (and in the open-forest surrounding site F) were smaller, single trunked trees approximately 14–22 m tall and of GBH approximately 1.0–1.5 m.

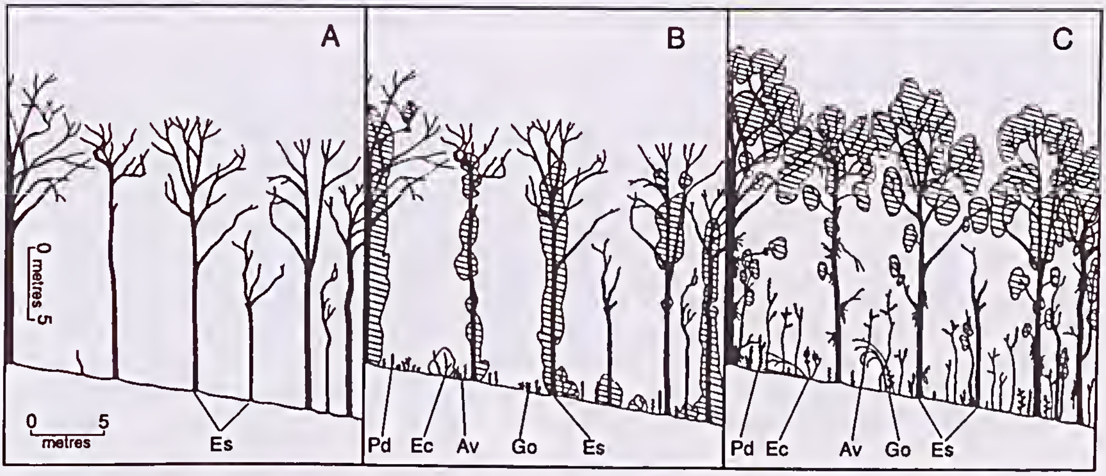


Fig. 3. Vegetation profiles in open-forest (subsite E1) immediately after the fire and 3 and 10 years later. Horizontal and vertical scales are the same. Hatching indicates the extent of canopy regrowth. A, Open-forest of *Eucalyptus tricarpa* (Es) immediately after the fire. B, 3 years after fire. Small coppicing trees of *Eucalyptus cypellocarpa* (Ec); *Pultenaea daphnoides* (Pd), *Acacia verticillata* (Av) and *Goodenia ovata* (Go) are present in the shrub stratum. C, 10 years after fire.

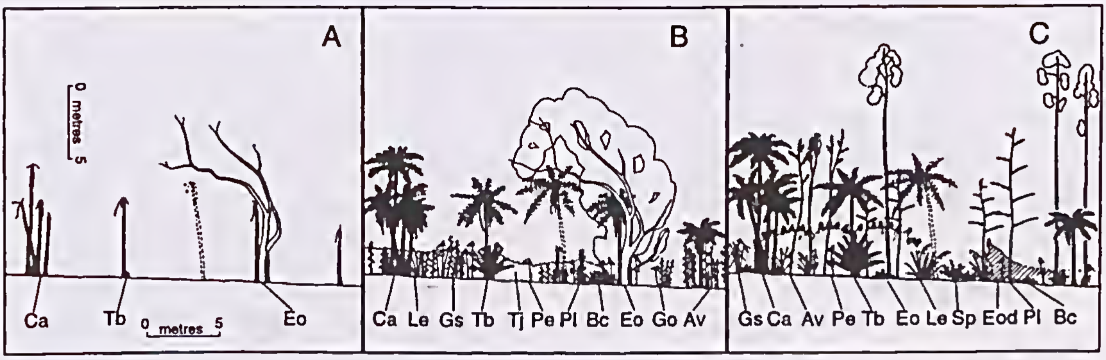


Fig. 4. Vegetation profiles in a gully complex (subsite F1) immediately after the fire and 3 and 10 years later. Horizontal and vertical scales are the same. A, *Eucalyptus obliqua* (Eo) gully complex immediately after the fire with *Cyathea australis* (Ca) and *Todea barbara* (Tb) present in the understorey. B, 3 years after fire. *Lepidosperma elatius* (Le), *Gahnia sieberiana* (Gs), *Tetrarrhena juncea* (Tj), *Pteridium esculentum* (Pe), *Prostanthera lasianthos* (Pl), *Goodenia ovata* (Go), *Acacia verticillata* (Av) and *Blechnum cartilagineum* (Bc) are present in the understorey. C, 10 years after fire. *Spyridium parvifolium* (Sp) and dead *Eucalyptus obliqua* (Eod).

Subsite Vegetation type	E1 Open forest	E2 Open forest	E3 Gully complex	F1 Gully complex	F2 Modified gully complex
Eucalypts* (species)	Et	Et Ec Ea Ew Eo	Ec	Eo	Eo Ew
Cover %					
Prefire (approx.)	30-70	30-70	30-70	30-70	30-70
3 years	<10	<10	30	30	70
10 years	30-70	30-70	30-70	30-70	70
Height (m)					
Prefire (approx.)	18.2	17.2	36.0	14.0	14.0
Live stem height after fire (Year 0)	14.2	13.2	30.0	12.0	0.0
3 years	14.6	13.9	32.0	14.0	5.0
10 years	16.8	16.5	34.0	14.1	18.0
Length of Epicormics (m)					
3 years: Base	0.80	0.52	–	–	–
3 years: Trunk	0.45	1.33	3.5	3.0	–
3 years: Crown	0.94	0.90	2.5	2.5	–
Understorey					
Cover %					
Prefire (approx.) - all plants	10-30	30-70	30-70	30-70	30-70
3 years: shrubs	25.0	25.0	30.0	10.0	1.0
3 years: moss	–	30.0	1.0	1.0	1.0
3 years: ferns	–	–	38.5$^{¥}$	19.7$^{\delta,¥,!}$	10.0$^{¥}$
3 years: all plants	26.5	62.5	>82.5	77.5	15.0
3 years: bare ground	73.5	37.5	<17.5	22.5	85.0
10 years: trees (<4 m)	–	–	tr	–	tr
10 years: shrubs	60.0§	50.0§	50.0	10.0	tr
10 years: sedges/rushes	tr	15.0	tr	5.0	2.0
10 years: grasses	tr	15.0	30.0	–	1.0
10 years: other herbs	tr	tr	tr	– tr	tr
10 years: ferns	–	–	tr	45.0 –	1.0
10 years: mosses etc	tr	tr	tr	tr	1.0
10 years: all plants	60.0	80.0	80.0	50.0	5.0
10 years: litter	20.0	20.0	20.0	40.0	75.0
10 years: bare ground	20.0	–	–	–	20.0
Height (m)					
Prefire (approx.)	3.0	3.0	3.0$^{\phi}$	4.5$^{\delta}$, 5.5†	4.5$^{\delta}$, 5.5†
Live stem height after fire (Year 0)	0.00	0.00	0.00	4.5$^{\delta}$, 0.0†	0.0, 0.0
3 years	2.0	2.5	2.0$^{¥}$	4.5$^{\delta}$, 1.0†	1.8$^{¥}$
10 years	3.8§	4.2§	6.0$^{\phi}$	5.3$^{\delta}$, 5.9†	2.0$^{\#}$, 1.8$^{¥}$

Table 4. Structure of forest and gully plant communities 3 and 10 years after fire. *Tallest stratum, Et=*Eucalyptus tricarpa*, Ec=*Eucalyptus cypellocarpa*, Ea=*Eucalpytus aromaphloia*, Ew=*Eucalpytus willisii*, $^{\phi}$=*Pomaderris aspera*, †=*Prostanthera lasianthos*, $^{\delta}$=*Cyathea australis*, $^{!}$=*Todea barbara*, $^{¥}$=*Pteridium esculentum*, $^{\#}$=*Spyridium parvifolium*, §=*Acacia verticilliata*, tr=trace.

(e) Introduced species. Eleven introduced species were present at low density either near creeks (subsites E3, F1 and F2; *Aster subulatus, Briza minor, Sonchus oleraceus*), close to roads (subsites E1 and E2; *Anthoxanthum odoratum, Hypochoeris radicata, Stellaria media, Vulpia myuros*) or both (subsites E1, E2, E3, F1 and F2; *Aira caryophyllea, Isolepis hystrix, Centaurium spicatum, Cirsium vulgare*).

(f) Non-vascular plants. In all communities, non-vascular plants were common colonizers of bare ground in the first 6 months after fire. They established apparently from wind-borne spores, growing in areas where the upper 2 cm of ash-rich surface soil had not been removed by wind or sheet erosion. A definite sequence of species was seen which was particularly noticeable on damper southerly slopes of open-forest (subsite E2, Table 3) where whole hillsides were colonised by the liverwort *Marchantia berteroana* and the moss *Funaria hygrometrica* and the fungus *Gerronema postii* in the first 6–8 months after fire. During year 2, *F. hygrometrica* was replaced by another moss, *Ceratodon purpureus*, and then in year 3 by a greater variety of species including *Barbula calycina, Campylopus introflexus* and *Polytrichum juniperinum* (Table 3). A similar sequence of mosses was seen at drier forest sites (subsite E1), in gully complexes (subsites E3 and F1), and on burnt peat following initial colonisation by *M. berteroana* (Table 3).

By year 3, ground covered by bryophytes in Ironbark forest ranged from 10% on dry eroded north facing slopes (subsite E1) to 25–75% in damper south facing slopes (subsite E2, Table 4).

Structure. At all sites, the fire completely incinerated the understorey and crown fired the overstorey, killing the top 4.0 m of the *E. tricarpa* canopy on the upper slopes and the top 6.0 m and 2.0 m of the *E. cypellocarpa* and *E. obliqua* canopies in the gullies. Very small trees (girth <35 cm) were burnt to the ground. Some 4–6 m trees of the understorey were killed above ground then produced root suckers (eg. *Exocarpos cupressiformis, Acacia melanoxylon*); others (eg. *P. lasianthos*) were completely killed.

The overstorey and understorey at all sites began to re-establish in the first year after fire (Table 4, Figs 3–6).

(a) E. tricarpa *open-forest* (subsites E1 and E2; Table 4, Figs 3, 5A, 6A). Ninety per cent of eucalypt individuals survived the fire and vegetative regrowth commenced within 2–3 months. *E. tricarpa* of GBH greater than 0.5 m pre-fire sprouted from epicormic buds at the base or trunk, whereas trees of less than 0.2 m GBH sprouted from the base only. No significant changes in girth were observed in the first 3 years after fire. In open-forest communities during years 1–3, basal epicormics of eucalypts contributed significantly to vegetation cover and were more common on trees on dry, upper northerly facing slopes, than in moister sites.

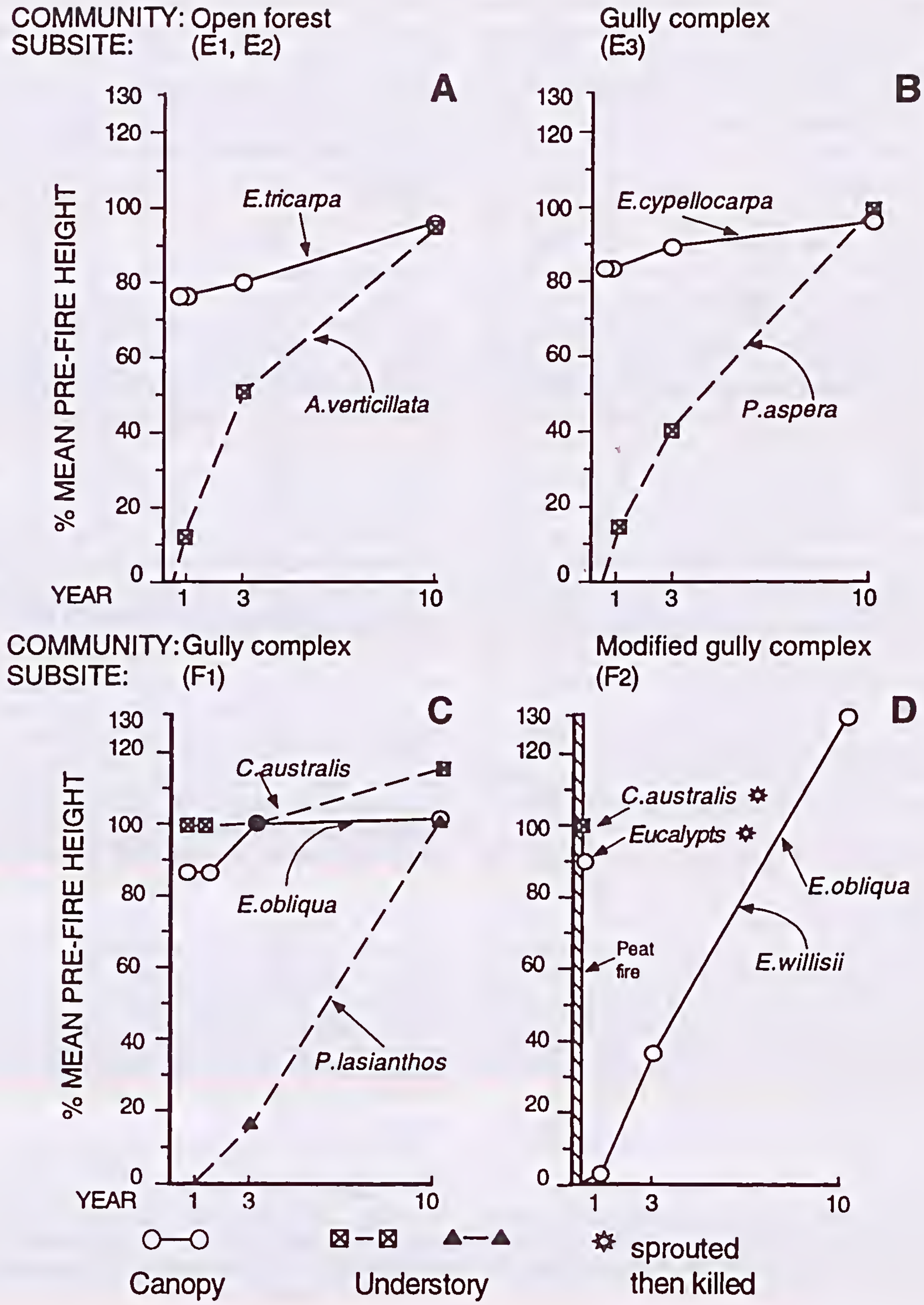
Rate of recovery of *E. tricarpa* canopy height and cover (relative to approximate original height and cover) was slower than that of the eucalypts in the gully complexes (Table 4, Figs 3, 4).

Crown recovery was slow in *E. tricarpa* open-forest; almost no canopy regrowth was seen by year 3 (Table 4, Fig. 3). By year 10, the eucalypt overstorey had recovered reaching approximate pre-fire height and estimated cover values (Table 4, Figs 3, 5A). Density of seedling eucalypts at subsites E1 and E2 was 3000–6000/ha 8 months after the fire, 200–600/ha 3 years after the fire, and approximately 100/ha 10 years after fire.

The understorey of the *E. tricarpa* open-forest communities (site E), changed in both structure and species composition following the fire. Prior to the fire the understorey in most of the forest had been open, grassy and dominated by *Poa sieberiana* (Parsons et al. 1977; Wark, pers. obs.). A few senescent shrubs of hard-seeded species such as *Acacia verticillata* and *Pultenaea daphnoides* were found on the lower slopes near creeks. Following the wildfire, massive germination of seedlings of *A. verticillata, P. daphnoides* and *Goodenia ovata* occurred during year 1 at site E. This germination produced two crops of seedlings at approximately 2–6 and 12–18 months, seedlings establishing among the carpets of mosses and liverworts on the thin top soil that remained following soil erosion.

The new shrub layer grew rapidly in the early years after fire, and by year 3 formed a dense, prickly, understorey. It reached approximately 4.0 m by 10 years (Table 4, Figs 3, 5A, 6A), becoming spindly and senescent by 13 years. By year 10, the three main shrubs, *Acacia verticillata, Goodenia ovata* and *Pultenea daphnoides*, had reached heights of 3.8 m, 1.4 m and 1.9 m respectively at subsite E1.

The grassy (*Poa sieberiana*) understorey, seen pre-fire, did not reappear in the 10 years after the fire. However, on damper southerly slopes, on silty clay (subsite E2), wire grass (*Tetrarrhena juncea*) and thatch saw-sedge (*Gahnia radula*) re-established, and were significant cover components during the 10 years (Fig. 6A).


COMMUNITY: Open forest
SUBSITE: (E1, E2)
A
% MEAN PRE-FIRE HEIGHT
E.tricarpa
A.verticillata
YEAR
Gully complex
(E3)
B
E.cypellocarpa
P.aspera
COMMUNITY: Gully complex
SUBSITE: (F1)
C
C.australis
E.obliqua
P.lasianthos
Modified gully complex
(F2)
D
C.australis
Eucalypts
Peat fire
E.obliqua
E.willisii
Canopy
Understory
sprouted then killed

In open-forest the number of herbaceous species present decreased during the 10 years to 43% of the year 1–3 level (97 years 1–3; cf. 42 year 10, Table 3).

(*b*) *Gully complexes* (subsites E3 and F1; Table 4, Figs 4, 5B, 5C, 6B, 6C). About 90% of eucalypts in gully complexes survived the fire. Regrowth of 36.0 m tall *Eucalyptus cypellocarpa* (GBH pre-fire >1.5 m) and 14.0 m tall *E. obliqua* (GBH pre-fire >1.0 m) was by epicormic regrowth from the crown and upper branches; crown recovery occurring by 10 years (Table 4, Figs 4, 5B, 5C). Surviving *E. cypellocarpa* of GBH <0.4 m sprouted from the base only. At subsite F1, two 14.0 m *E. obliqua* sprouted following the fire, grew vigorously for 3 years, then fell (Fig. 4).

At subsite F1, 92% of *Cyathea australis* (5.0 m tall; range 4.5–6.0 m) survived the fire and sprouted from the crown 3 weeks post-fire, growing 0.8 m in the 10 years post-fire (Figs 4, 5C).

At subsite E3 the previous understorey of *Pomaderris aspera* and *Prostanthera lasianthos* re-established from seed in the 10 years after fire (Table 4, Fig. 5B). Similarly, at subsite F1, the *P. lasianthos* understorey re-established in the 10 years reaching approximate pre-fire height and cover (Table 4, Fig. 5C). By year 10, the mean height of seedling shrubs of *P. lasianthos* at subsite F1 was 5.9 m (range 4.9–9.0 m). At both sites, *Pteridium esculentum* contributed significantly to substratum cover in years 1–3, then was rarely seen (Figs 6B, 6C). *Tetrarrhena juncea* was also a significant cover component till

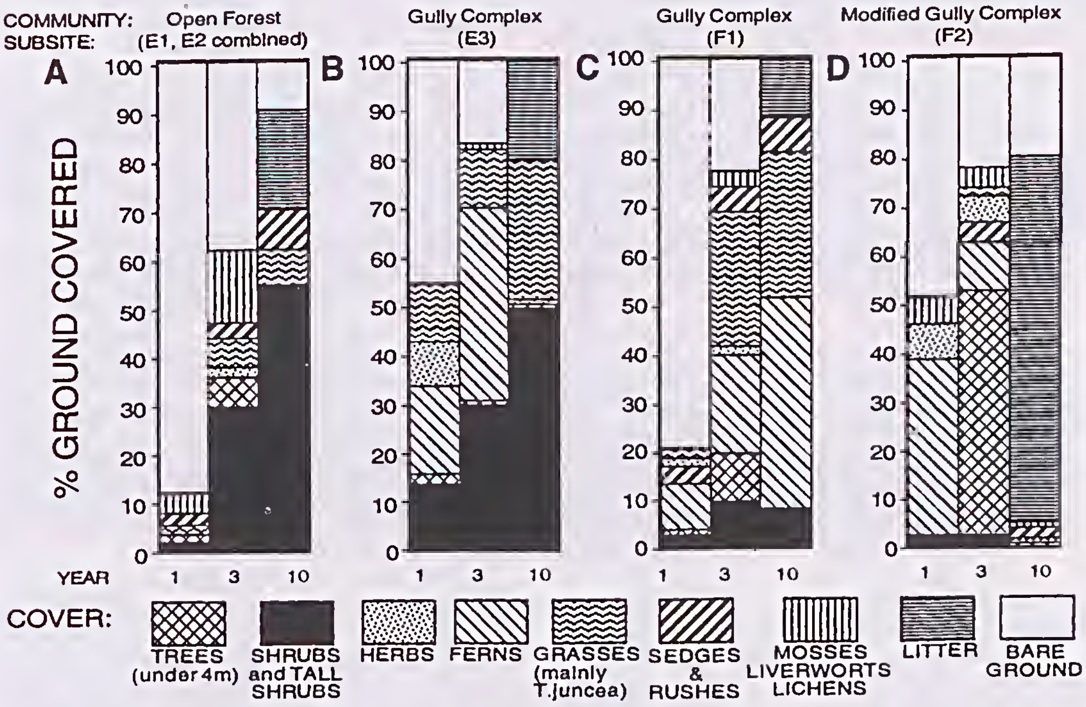


Fig. 6. Cover of shrub stratum and ground stratum of open-forest and gully complexes 1, 3 and 10 years after fire. *Tetrarrhena juncea* (*T. juncea*). A, Open-forest (subsites E1 and E2 combined). B, Gully complex (subsite E3). C, Gully complex (subsite F1). D, Modified gully complex (subsite F2).

Fig. 5. Recovery of height of the tree stratum (canopy) and shrub stratum (understorey) 1, 3 and 10 years after fire. A, Open-forest (subsites E and E2 combined). *E. tricarpa=Eucalyptus tricarpa*; *A. verticillata=Acacia verticillata*. B, Gully complex (subsite E3). *E. cypellocarpa=Eucalyptus cypellocarpa*; *P. aspera=Pomaderris aspera*. C, Gully complex (subsite F1). *E. obliqua=Eucalyptus obliqua*; *C. australis=Cyathea australis*; *P. lasianthos=Prostanthera lasianthos*. D, Modified gully complex (subsite F2). *E. obliqua=Eucalyptus obliqua*; *E. willisii=Eucalyptus willisii*; *C. australis=Cyathea australis*.

year 10, growing vigorously in sunny areas (Figs 6B, 6C). The filmy fern, *Hymenophyllum cupressiforme*, recorded at subsite F1 before the fire, was not seen in the 10 years post-fire.

Eucalypt seedlings germinated in open areas at subsite F1, reaching densities of 14 000/ha at year 3, and 140/ha at year 10, and mean height of 5.0 m and 18.0 m at years 3 and 10 respectively. Seedlings shaded by *Cyathea australis* or *Todea barbara* reached only a height of 2.0 m by year 3, and did not survive till year 10. In contrast, at subsite E3, where conditions were drier and *P. esculentum* cover denser, eucalypt seedling density at years 3 and 10 years was 200/ha and approximately 20/ha respectively.

(c) Modified gully complex (subsite F2; Table 4; Figs 5D, 6D). Major structural changes were observed at this subsite when a peat fire was ignited by the Ash Wednesday wildfire and continued to burn for 3 months. Mature 5.0 m tall *Cyathea australis* and 14.0 m tall *Eucalyptus obliqua* which survived the wildfire and sprouted at 3 and 8 weeks respectively, were burnt by the peat fire, and died and fell at 3.0–3.5 months post-fire (when the *C. australis* fronds were 1.5 m long and the *E. obliqua* epicormic growth 0.3 m in length; Fig. 5D).

Death of regenerating plants following the peat fire resulted in a dry open sunny area. *Pteridium esculentum* invaded the site (from the unburnt peat at subsite F1) and with fire mosses dominated the area by year 1. Many eucalypt seedlings germinated in this open area during year 1, covering the site, and seedling density at 3 and 10 years was 37 000/ha and 10 000/ha respectively. The two main species present at year 3 were *E. obliqua* (20 000/ha) and *Eucalyptus willisii* (17 000/ha). The young plants grew rapidly, reaching a mean height of 5.0 m by year 3 and 18.0 m (GBH 82 cm) by year 10 (Table 4). By year 10, the eucalypt seedling population had formed a new overstorey, replacing the *Eucalyptus obliqua* and *E. willisii* killed by the peat fire (Fig. 5D). The understorey beneath these trees was extremely simple and sparse (5% cover) and contained little *P. esculentum*, little moss and an occasional shrub (Fig. 6D).

The previous understorey of *Cyathea australis* and *Prostanthera lasianthos* never re-established during the 10 years post-fire (Fig. 5D). Only two plants of *P. lasianthos* 5.0 m tall and one plant of *C. australis* 0.1 m tall were found at the site at year 10.

Though understorey cover of vascular and non-vascular plants on the burnt peat (subsite F2) 3 years post-fire was approximately the same as that of the adjacent gully community (subsite F1), total species richness at subsite F2 (years 1–3 combined) was 45% of that at subsite F1. By year 10, total understorey plant cover at subsite F2 was about 5%, and total plant species richness about 60% of that in the adjacent gully complex.

A total of 14 species of vascular plants and 12 species of bryophytes (mainly mosses) were found on the burnt peat at year 10 (Table 3). Fallen trees and tree ferns, killed by the peat fire, formed a tangled layer of litter (Table 4, Fig. 6D). Most bryophyte growth was on charred, fallen trunks of dead eucalypts or *C. australis*, rather than on the burnt peat, which by 10 years was covered by a 2 cm layer of humus and dead leaves.

Regeneration strategies

(a) Regeneration mechanisms and timing. Regeneration was either by regrowth (from dormant buds, in stems, lignotubers, root tussocks, roots, rhizostolons, rhizomes, corms, tubers and tuberoids) from seed or propagules, or by both means (Table 5).

The first species to appear following the fire regenerated mainly by regrowth and included the ferns *Cyathea australis*, *Pteridium esculentum* and *Todea barbara* at three weeks, and sedges, rushes and other herbaceous species from four to five weeks. Regrowth of eucalypts commenced between two to three months. As mentioned earlier, the fire moss *Funaria hygrometrica*, the liverwort *Marchantia berteroana*, and fruiting bodies of the fungus *Gerronema postii* appeared 6–8 months after the fire, often forming extensive carpets on sheltered, damper slopes.

The three most conspicuous shrubs (*Acacia verticillata*, *Goodenia ovata* and *Pultenaea daphnoides*) germinated from seed between 2 and 6 months; and both north and south facing slopes in the ironbark forest looked like giant seed beds. By the end of year 1, all species capable of vegetative regrowth, and three-quarters of species which regenerated from seed, had appeared.

(b) Regeneration strategies and life form groups. Regeneration strategies and life form groups of all vascular species present 1–3 years post-fire and surviving till year 10 are shown in Table 6.

About 26% of vascular plant species regenerated only by regrowth (ORR) including sedges, rushes, lilies, orchids and Droseraceae. About 38% re-

Obligate seed regenerators † (from seed or spores or propagules only)	Regen. strategy	First flowering
Tall shrubs		
Acacia dealbata	S1	
Acacia mearnsii	S1	
Acacia pycnantha	S1	F2
Pomaderris aspera	S1	
Pomaderris elachophylla	S1	F3
Pomaderris ferruginea	S1	
Prostanthera lasianthos	S1	
Lichens		
Cladia aggregata	S2	
Liverworts		
Asterella drummondii	S3	F3
Anthoceros laevis	S3	F3
Cephaloziella exiliflora	S3	F3
Lethocolea pansa	S3	F3
Lophocolea semiteres	S3	F3
Marchantia polymorpha	S1	F1
Symphogyna podophylla	S3	F3
Mosses		
Barbula calycina	S3	F3
Bryum billardierei	S3	F3
" *pachytheca*	S3	F3
Breutelia affinis	S3	F3
Campylopus introflexus	S3	F3
" *pyriformis*	S3	F3
Ceratodon purpureus	S2	F2
Funaria hygrometrica	S1	F1
Polytrichum juniperinum	S3	F3
Wijkia extenuata	S3	F3
Grasses		
**Aira caryophyllea*	S1	F1
**Briza minor*	S1	F1
Echinopogon ovatus	S1	F1
**Vulpia myuros*	S1	F1
Shrubs		
Acacia acinacea	S1	F3
" *genistifolia*	S1	F3
" *mucronata*	S1	F3
" *myrtifolia*	S1	F3
" *verniciflua*	S1	F3
" *verticillata*	S1	F3
Correa reflexa	S1	F2
Epacris impressa	S1	F2(?)
Goodenia ovata	S1	F1
Ozothamnus ferrugineus	S1	F2
Indigofera australis	S1	F2
Olearia lirata	S1	F2(?)
" *phlogopappa*	S1	F2
" *ramulosa*	S1	F2

Facultative regrowth regenerators † (by regrowth, and from seed or propagules)	Regeneration strategy		First flowering
Trees			
Eucalyptus aromaphloia	St1, L1	S1	
" *baxteri*	St1, L1	S1	F2
" *cypellocarpa*	St1, L1	S1	
" *globulus* ssp. *bicostata*	St1, L1	S1	
" *obliqua*	St1, L1	S1	F2
" *ovata*	St1, L1	S1	
" *tricarpa*	St1, L1	S1	F3
" *viminalis*	St1, L1	S1	
" *willisii*	St1, L1	S2	F3
Tall shrubs			
Acacia melanoxylon	Rsk1, L1	S1	
Exocarpos cupressiformis	Rsk1, L1	S1	
Ferns & allies			
Adiantum aethiopicum	R1	S2	F2
Blechnum cartilagineum	R1	S2	F2
" *nudum*	R1	S2	
Cyathea australis	R1	S2	F1
Gleichenia microphylla	R1	S2	F2
Hymenophyllum cupressiforme ¥	?	?	?
Hypolepis rugosula	R1	S2	F2
Pteridium esculentum	R1	S2	F2
Todea barbara	R1	S2	F1
Grasses			
Agrostis avenacea	R1	S1	F1
**Anthoxanthum odoratum*	R1	S1	F1
Austrostipa rudis	R1	S1	F1
" *semibarbata*	R1	S1	F1
Danthonia geniculata	R1	S1	F1
" *induta*	R1	S1	F1
" *pilosa*	R1	S1	F1
" *procera*	R1	S1	F1
" *setacea*	R1	S1	F1
Deyeuxia densa	R1	S1	F1
" *quadriseta*	R1	S1	F1
Dichelachne rara	R1	S1	F1
**Holchus lanatus*	R1	S1	F1
Joycea pallida	R1	S1	F1
Microlaena stipoides	R1	S1	F1
Notodanthonia semiannularis	R1	S1	F1
Tetrarrhena distichophylla	R1	S1	F1
" *juncea*	R1	S1	F1
Poa morrisii	R1	S1	F1
" *sieberiana*	R1	S1	F1
" *tenera*	R1	S1	F1
Shrubs			
Acrotriche serrulata	L1	S1	F2
Astroloma humifusum	L1	S1	F2

Table 5 continued next page (see legend on page 29)

Obligate seed regenerators † (from seed or spores or propagules only)	Regen. strategy	First flowering
" *teretifolia*	S1	F2
Pultenaea daphnoides	S1	F2
" *scabra*	S1	F2
Pimelea humilis	S1	F1
" *linifolia*	S1	F2
Leptospermum continentale	S2	F2?
Solanum laciniatum	S1	F2
Spyridium parvifolium	S1	F2
Herbs		
Acaena novae zelandiae	S1	F2
Amyema pendulum ¥	?	?
Asperula scoparia	S1	F2
**Aster subulatus*	S1	F1
**Centaurium spicatum*	S1	F1 or F2
**Cirsium vulgare*	S1	F1
Dichondra repens	S1	F2
Geranium solanderi	S1	F1
Euchiton involucratus	S1	F2
" *sphaericus*	S1	F2
Gonocarpus tetragynus	S1	F1
Galium binifolium	S1	F2
Geranium spp.	S1	F2
Hydrocotyle callicarpa	S1	F1
" *hirta*	S1	F2?
" *laxiflora*	S1	F2?
Hypericum gramineum	S1	F1
Lobelia rhombifolia	S1	F1
Opercularia varia	S1	F1
Phyllanthus gunnii	S2?	F3?
Poranthera microphylla	S1	F1
Rorippa dictyosperma	S1	F1
Senecio velleioides	S1	F2
Senecio spp.	S1	F1
Stellaria flaccida	S1	F1
" *pungens*	S1	F2
" *media*	S1	F2?
Viola hederacea	S1	F1
" *cleistogamoides*	S1	F1
Wahlenbergia gracilienta	S1	F1
" *stricta*	S1	F1
Creepers & climbers		
Billardiera scandens	S1	F2
Cassytha glabella	S1	F2
" *melantha*	S2	F2
Clematis aristata	S1	?
Comesperma volubile	S1	F1
Glycine clandestina	S1	F2
Kennedia prostrata	S1	F1

Facultative regrowth regenerators † (by regrowth, and from seed or propagules)	Regeneration strategy		First flowering
Bursaria spinosa	L1	S1	F2
Coprosma quadrifida	L1	S1	
Hibbertia riparia	L1	S1	F2
Lissanthe strigosa	L1	S2	F2
Lomatia ilicifolia	L1	S1 rare	F1
Melaleuca squarrosa	L1	S1 rare	F2?
Olearia argophylla	L1	S2	F3?
Herbs			
Brunonia australis	R1	S1	F1
**Carduus tenuiflorus*	R1	S1	F1
Cynoglossum suaveolens	R1	S1	F1
Goodenia lanata	R1	S1	F1
Helichrysum leucopsideum	R1	S1	F1
" *scorpioides*	R1	S1	F1
Lagenifera gracilis	R1	S1	F1
" *stipitata*	R1	S1	F1
Leptorhynchos linearis	R1	S1	F1
" *squamatus*	R1	S1	F1
**Oxalis corniculata*	R1	S1	F1
Pelargonium australe	R1	S1	F1
Plantago varia	R1	S1	F1
**Sonchus oleraceus*	R1	S1	F1
Veronica calycina	R1	S1	F1
Veronica derwentiana	R1	S1	F2

Obligate regrowth regenerators † (by regrowth only)	Regeneration strategy	First flowering
Sedges & rushes		
Gahnia radula	R1	F2
" *sieberiana*	R1	F2
**Isolepis hystrix*	R1	F1
" *indundata*	R1	F1
" *marginata*	R1	F1
Juncus pauciflorus	R1	F2
" *planifolius*	R1	F1
Lepidosperma elatius	R1	F2
Luzula meridionalis	R1	F1
Schoenus apogon	R1	F1
Orchids		
Acianthus caudatus	Tu1	F1
" *pusillus*	Tu1	F1
Caladenia cardiochila	Tu1	F1
Caladenia catenata	Tu1	F1
" *tentaculata*	Tu1	F1
" *menziesii*	Tu1	F1
" *reticulata*	Tu1	F1
Cyrtostylis reniformis	Tu1	F1
Dipodium punctatum	Tu1	F1
Eriochilus cucullatus	Tu1	F1
Prasophyllum odoratum	Tu1	F1

Table 5 continued next page (see legend on page 29)

Obligate regrowth regenerators † (continued) (by regrowth only)	Regeneration strategy	First flowering
Pterostylis longifolia	Tu1	F1
" *nutans*	Tu1	F1
" *nana*	Tu1	F1
" *parviflora*	Tu1	F1
" *sanguinea*	Tu1	F1
Thelymitra flexuosa	Tu1	F1
" *ixioides*	Tu1	F1
" *pauciflora*	Tu1	F1
" *rubra*	Tu1	F1
Lilies & irises		
Burchardia umbellata	T1	F1
Caesia parviflorus	T1	F1
Dianella revoluta	T1	F2
Lomandra filiformis	T1	F1
" *longifolia*	T1	F1
" *micrantha*	T1	F1
" *multiflora*	T1	F1
Thysanotus juncifolius	T1	F1
" *tuberosus*	T1	F1
" *patersonii*	T1	F1
Herbs		
Drosera peltata		
ssp. *auriculata*	T1	F1
" *macrantha*	T1	F1
" *peltata*	T1	F1
" *whittakerii*	R1	F1
**Hypochoeris radicata*	R1	F1
Lobelia gibbosa	R1	F1

Table 5. Regeneration strategies and flowering of forest and gully communities 1–3 years after fire. *Key:* Regeneration strategy/year—S1=germinated from seed year 1; S2=germinated from seed year 2; S3= germinated from seed year 3; R1=regrowth from rhizomes year 1; R2=regrowth from rhizomes year 2; T1=regrowth from tubers year 1; Tu=regrowth from tuberoids year 1; L1=regrowth from lignotubers year 1; St1=regrowth from stems year 1; C1=regrowth from corms year 1; RSt1=regrowth from rhizostolons year 1; Rsk1=regrowth from root suckers year 1. Flowering/ year—F1=first flowered year 1; F2=first flowered year 2; F3=first flowered year 3. †Terminology follows Purdie (1977a, 1977b). Seed is used to mean both seeds and spores. ¥=Present before fire, but not recorded 1–10 years after fire.

generated only from seed (OSR species) and were mainly shrubs and herbs. The remaining 36% were FRR species, regenerating both by regrowth and from seed, and included all trees, as well as shrubs, ferns and herbs (Table 6).

Approximately 62% of all vascular species which appeared in the first 3 years were sprouting species (ORR and FRR; Table 6). The other 38% were, as mentioned earlier, OSR species. A similar proportion (40%) of OSR species remained at year 10, in fact about 73% of all shrub species present at years 1–3 and remaining till year 10 were OSR (29 of 40, years 1–3; 24 of 33, year 10; Table 6).

About 48% of herbaceous species and 83% of shrub species present immediately after fire were still present at year 10.

Aerial parasites such as *Amyema pendulum* did not reappear in the 10 years after the fire. Root parasites such as *Exocarpus cupressiformis* regenerated both vegetatively and from seed, but died between years 3 and 7.

(c) Regeneration strategies of trees and shrubs. About 40% trees and shrubs were FRR regenerators, including all eucalypt species (Table 5). Some FRR shrubs, such as *Acacia melanoxylon*, showed only small amount of rootstock regeneration germinating mainly from seed. Others, like *Exocarpos cupressifonnis* and *Olearia argophylla*, regenerated in approximately equal numbers by regrowth (from lateral roots or the base of the trunk) or from seed. Species such as *Bursaria spinosa* regenerated mainly by regrowth. No shrubs regenerated by regrowth exclusively.

Sixty per cent of trees and shrubs regenerated from seed only. In the Ironbark forest, where a shrub layer had not been present in the years before the fire, densities of shrub seedlings 1 year after fire were *A. verticillata* 23 seedlings/m^2, *G. ovata* 25 seedlings/m^2, *P. daphnoides* 10 seedlings/m^2. Many of these seedling shrubs died during the dry summer period, and densities at year 3 were 10 seedlings/m^2, 9 seedlings/m^2, and 6 seedlings/m^2 respectively (100 000/ha, 90 000/ha, 60 000/ha).

(d) Regeneration strategies on burnt peat. With the exception of *Pteridium esculentum* and *Tetrarrhena juncea* (both of which invaded by rhizomes from outside), all species which established on the burnt peat (subsite F2) regenerated either from seed or spores. All 14 species of vascular plants which appeared on the burnt peat in the 10 years following the fire were present in either the adjacent gully complex (subsite F1) or the neighbouring 18–20 m tall *E. obliqua/E. willisii* heathy open-forest following the fire (eg. *Spyridium parvifolium*). One introduced species (*Aster subulatus*, present subsite F1) regenerated on the burnt peat in the 10 years following the fire.

Species present Regeneration strategy post fire	Years 1-3 OSR	 FRR	 ORR	Year 10 OSR	 FRR	 ORR	
Trees (9)*	-	9	-	-	7	-	
Shrubs (40)	29	11	-	24	9	-	
Dicotyledon herbs (52)		29	16	6	12	6	4
Monocotyledon herbs (65)							
Orchids (20)	-	-	20	-	-	9	
Lilies & irises (10)	-	-	10	-	-	6	
Grasses (25)	4	21	-	-	6	-	
Sedges & rushes (10)	-	-	10	-	-	3	
Creepers & climbers (7)	7	-	-	3	-	-	
Ferns (8)	-	8	-	-	8	-	
Subtotal	69	65	46	39	36	22	
% Total species $^{\delta}$	38%	36%	26%	40%	37%	23%	
Total species $^{\delta}$		180			97		

Table 6. Regeneration strategies and life form groups of all vascular plant species appearing 1–3 years post-fire and still present 10 years post-fire. *Key:* OSR=obligate seed regenerators; FRR=facultative regrowth regenerators; ORR=obligate regrowth regenerators. Terminology follows Purdie (1977a, 1977b). *Numbers in parentheses show total species present years 1–3; $^{\delta}$total species=total number of species recorded (quadrat and site data combined).

Flowering response after fire

(a) *Response during first spring.* Sixty per cent of species (94 of 157) which regenerated during year 1 flowered or produced spores (Table 5). Of these, 87 species were herbs. The rest included 2 ferns, 2 bryophytes, a fungus and 3 species of shrubs.

About 82% of all herbs recorded (including sedges, rushes, grasses, orchids, lilies, creepers and climbers) flowered in the first year after fire, and almost all the rest by year 2. Some ORR herbs, including autumn and winter-flowering orchids (*Acianthus pusillus, Eriochilus cucullatus, Pterostylis parviflora*), flowered from 5 months post-fire, as did *Drosera whittakeri* and *Lagenifera gracilis.*

There was conspicuous production of fruiting bodies by the moss *Funaria hygrometrica*, the liverwort *Marchantia berteroana*, and the fungus *Gerronema postii* from 6 months post-fire. By late spring, whole hillsides of the open-forest in damp areas (such as subsite E2) were coloured yellowish green by a carpet of fruiting bryophytes.

Grasses were conspicuous in the first spring after fire. Twenty-three species were identified at open-forest sites including 5 species of *Danthonia* (Table 3). Some species (eg. *Danthonia induta* and *D. procera*) flowered prolifically then were not seen in later years. Only 5 species of grasses were recorded in open-forest by year 10 (Table 3).

(b) *Orchid flowering response.* Nineteen species of terrestrial orchids appeared and flowered in open-forest during the first 3 years after fire. Though 16 species of orchids were recorded at subsite E1 during the 10 years, only 4 species appeared and flowered on this dry, eroded slope during year 1 (Table 3). Field observations suggest that the density of year 1 flowering of most species was higher than in pre-fire years.

Flowering of some orchid species was stimulated by fire. Two species (*Caladenia menziesii* and *Prasophyllum odoratum*), which appear but rarely flower in normal years, bloomed prolifically the spring after the fire. Seed-set accompanied post-fire flowering for all orchid species during years 1–3.

Only 3 species of orchids (*Acianthus pusillus, Pterostylis nana, P. nutans*) were recorded in the gully communities prior to the fire and in the 10 years post-fire. Field records made in similar communities near Moggs Creek prior to the fire, list 11 gully species (*Acianthus caudatus, A. pusillus, Chiloglottis valida, Corybas dilatatus, C. incurvis, Cyrtostylis reniformis, Pterostylis curta, P. longifolia, P. nana, P. nutans, P. pedunculata*— M. White; M. MacDonald, pers. comm.), all of which have been observed in the 10 years post-fire.

(c) Flowering response of trees and shrubs. Three shrubs (*Goodenia ovata, Pimelea humilis, Lomatia ilicifolia*) flowered in the first year. All other shrubs (92%) did not commence flowering till years 2 or 3, or later (Table 5). *Lomatia ilicifolia* (which is rarely seen to flower except after fire) flowered on new regrowth at 6–8 months. The juvenile phase of some shrubs (eg. *Epacris impressa, G. ovata*) was brief; flowering occurring within 2 years on plants only a few centimetres high.

By year 3, about two-thirds of the vascular plant species had flowered, including 4 species of trees (*Eucalyptus baxteri, E. obliqua, E. tricarpa, E. willisii*) and 27 species of shrubs. Not flowering at year 3 were 5 species of trees (*Eucalyptus aromaphloia, E. cypellocarpa, E. globulus, E. ovata, E. viminalis*), and 7 species of tall shrubs (*Acacia dealbata, A. mearnsii, A. melanoxylon, Pomaderris aspera, P. ferruginea, Prostanthera lasianthos, Exocarpus cupressiformis*). All 12 species flowered by 10 years post-fire.

By year 3, the percentage of OSR shrubs and OSR herbs flowering was 83% and 97% respectively and most of these species appeared to set seed. Little seed predation was observed either on plants or the soil.

(d) Grazing during first 3 years. No grazing of vegetation by native or introduced mammals was seen in the first 2.5 years after fire; though European rabbits (*Oryctolagus cuniculus*) were observed browsing herbs at subsite E1 late in year 3, and swamp wallabies (*Wallabia bicolor*) browsing shrubs at subsite E2 during years 7 and 10. Heavy grazing of young shrubs of *Goodenia ovata* by unidentified insect larvae occurred at all sites during years 1 and 2, with about 50% of the leaves being eaten. Extensive grazing of *E. cypellocarpa* coppice regrowth (by sawfly larvae, *Perga* sp.) was seen at subsite E2 during year 3.

DISCUSSION

This study has shown that, after a long fire-free interval, an *E. tricarpa* open-forest in the Anglesea–Aireys Inlet district was resilient to a single severe summer surface wildfire, supporting observations of Gill (1975, 1981) for dry sclerophyll forests in southern Australia.

The regeneration patterns of the open-forest community conform to the 'initial floristic composition' models of Egler (1954), and Purdie & Slatyer (1976), as 99% of vascular plant species present prior to fire re-established during the first three years.

The increase in the number of species of non-vascular plants in both open-forest and gully communities, with time, and as vascular plant cover increased, is similar to that recorded for the Anglesea heaths and heath woodlands (Wark 1996). The decrease in vascular plant species richness, as vascular plant projective cover increased, is similar to that described by Specht and Specht (1989) for sclerophyll communities in southern Australia, and was also observed in the heaths and heath woodlands of the Anglesea area (Wark 1996).

The failure of *Amyema pendulum* and *Hymenophyllum cupressiforme* to re-establish in the Ironbark forest and the gully communities respectively in the 10 years following the wildfire is not unexpected. All plants of *A. pendulum* were killed, and the mistletoe bird, *Dicaeum hirundinacium* (which is responsible for seed distribution and was uncommon in the Angahook–Lorne State Park before the fire—Conole & Baverstock 1984; Gill 1994), has not been seen in the area in the 10 years since 1983 (P. Reilly, pers. comm.; Reilly 1991). Filmy ferns such as *H. cupressiforme*, were rare in the district before the fire and probably have not re-established because the climate in the gully complexes has become drier. It may take many years for a cool microclimate suitable for these delicate plants to develop. Ashton & Frankenberg (1976) and Chesterfield et al. (1991) have commented that *H. cupressiforme* is badly affected by wildfire. No *H. cupressiforme* plants were seen 5 years after the 1983 wildfire in warm temperate rainforest in East Gippsland, Victoria (Chesterfield et al. 1991), and only a few plants 25 years after the 1951 wildfire in cool temperate rainforest at Lily Pilly Gully, Wilsons Promontory National Park, Victoria (D. H. Ashton, pers. comm.).

In the *E. tricarpa* dry sclerophyll forest, 60% of all species which regenerated following this wildfire were sprouters (FRS or ORR species). Similar high proportions of vegetative regenerators have been described for dry sclerophyll forests in Western Australia (Christensen & Kimber 1975), and the Australian Capital Territory (Purdie & Slatyer 1976). The high proportion (40%) of OSR regenerators seen probably reflects the intensity of the wildfire. It is known that in dry sclerophyll forests in Western Australia and New South Wales high intensity fires stimulate germination of hard-seeded understorey shrubs and fireweeds (Christensen & Kimber 1975; Christensen et al. 1981; Auld & O'Connell 1991). The dense shrub understoreys (dominated by *Acacia* and *Pultenaea* spp.) which established throughout most of the open-forest communities of the Anglesea–Aireys Inlet region following the Ash Wednesday wildfire, replaced the previously more open, often grassy, understorey (Parsons et al. 1977). Field records (Pat Denham, pers. comm.) suggest that the seed which germinated forming the shrub understorey in the *E. tricarpa* open-forest may have been stored in the soil for over 30 years—possibly longer if previous fires were of insufficient intensity to stimulate germination.

The slow rate of crown recovery of the *E. tricarpa* open-forest in the first three years after fire, may have been a result of both moisture stress, and low nutrient status. Leitch et al. (1983) showed increased hydrophobic properties of the soil at a forest site near Warburton, Victoria, where extensive sheet erosion (and resulting soil nutrient losses) occurred following the Ash Wednesday wildfires. They commented that similar sheet erosion also occurred in some of the Otway forests following the Ash Wednesday fires, and our data supports this.

Both moisture and nutrients released from ash are necessary for establishment of early post-fire bryophyte colonisers such as *M. berteroana, F. hygrometrica* and *C. purpureus* (G. A. M. Scott, pers. comm.; Cremer & Mount 1965; Southorn 1977), and stimulate post-fire flowering in orchids (Pate & Dixon 1982). The reduced incidence of the early post-fire bryophytes at subsite E1, and the failure of 75% of the orchid species at this site to flower in the first year after fire, suggest that both moisture and certain nutrients were lacking in these exposed sites. In 1983, Barnett (1984) noted a decrease in flowering of some orchid species following a surface fire in a *Eucalyptus macrorhyncha* open-forest, on a steep site with heavy clay soils at King Lake, Victoria, and suggested that one factor which may have affected flowering was the removal, by soil erosion, of fire-released nutrients. Changes in the soil microflora after the fire may also have been a factor. Similarly, the failure of the parasitic tall shrub *E. cupressiformis* to survive on these dry sites after its early re-establishment from seed and by regrowth, suggests also that insufficient moisture and nutrients may have been available to the young plants in the early years after fire.

The open-forest described in the present paper may not be totally resilient to frequent severe wildfires if burning occurs before the primary juvenile period of some OSR species. In the Ironbark forest, 3 species of OSR tall shrubs (*Acacia mearnsii, A. dealbata, Pomaderris ferruginea*) had neither flowered nor set seed 3 years after the fire. If another fire occurred before they reached reproductive maturity, they could be eliminated. Parsons et al. (1977) have commented that repeated burning at frequent intervals may convert an open-forest with a shrub understorey to an open-forest with a grassy understorey. Coaldrake (1961) has observed similar changes following sequential fires in the coastal lowlands of southern Queensland.

In the gully complexes (where peat fires did not occur) 52% of the species which regenerated following the wildfire were OSR species, regenerating from seed only. Similar high proportions (50–60%) of obligate seed regenerators have been described for wet sclerophyll forests in Western Australia (Christensen & Kimber 1975), Victoria and New South Wales (Ashton 1981). The regeneration patterns of the Anglesea gully communities (in the absence of peat fires) also conformed to the initial floristic composition models of Egler (1954) and Purdie and Slatyer (1976) as 99% of vascular plant species present prior to the fire re-established during the first 3 years.

Like the *E. tricarpa* open-forest, the gully communities (where peat did not burn) may not be totally resilient to frequent severe wildfires.

By year 3, at least 4 OSR shrubs in each gully community had not flowered or set seed, including *Pomaderris aspera* and *Prostanthera lasianthos*. Seed of these species is stored in the soil, and *Pomaderris aspera* may be removed from an area if surface fires recur at intervals of less than 5–10 years (Ashton & Attiwill 1994). Burning of these areas twice within the primary juvenile period of these shrubs could result in their elimination.

The study has also shown that such dry gully communities may be extremely vulnerable to wildfire and that their floristics and structure may change dramatically if peat fires establish. In the 10 years following the peat fire, the *E. obliqua* gully complex with its *Prostanthera lasianthos*, *Cyathea australis* understorey has become a eucalypt monoculture with practically no understorey. It is likely that the seed source for recolonisation of the burnt peat was the surrounding *E. obliqua/E. willisii* open-forest, which contained 20 m eucalypts which had flowered and set seed the season before the wildfire. It was shown, after the Anglesea wildfires, that viable seed could survive in capsules of crown-fired *E. obliqua* (Ashton 1986). It is probable that seed shedding occurred onto the surface of the burnt peat after the in-ground fire was extinguished. Seeding in of *Spyridium parvifolium* probably also occurred from the surrounding open-forest. The presence of this shrub suggests the microclimate in both gully communities at site F is now drier than before the surface fire and the peat fire.

Hill & Read (1984) showed that the proximity of a sclerophyll seed source may result in significant changes in the species composition of the understorey of mixed eucalypt forests following humus fires in western Tasmania. They observed that species of sclerophyllous shrubs (*Leptospermum scoparium*, *Phebalium squameum*) found 150–400 m from their study area established from wind-dispersed seed on burnt peat.

In the present study it was found that, with the exception of two FRS species (*Pteridium esculentum*, *Tetrarrhena juncea*) which grew into the burnt peat after the fire ceased, all 12 other species of vascular plants found on the burnt peat at year 10 established from seed or spores shed into the area from the adjacent gully complex, or surrounding dry sclerophyll forest.

Because of the density of the eucalypt overstorey, and the changed hydrology of the area, it may be many decades, or even some hundreds of years, before an understorey of *Prostanthera lasianthos* and *Cyathea australis* re-establishes in the area of the peat fire. Burning of this area at 10 years, by either a low intensity fire or a wildfire, could result in reduction or elimination of any OSR gully species which have begun to re-establish, and the continued invasion of sclerophyllous species from the adjacent *E. obliqua* open-forest.

It is probable that the red material produced when the peat burnt had certain properties which favoured plant establishment and growth in the short term. A dense cover of ash-requiring mosses and liverworts (including *F. hygrometrica*, *C. purpureus* and *M. berteroana*—Southorn 1977) appeared on the burnt peat in the first 3 years after fire. Cremer & Mount (1965) and Duncan & Dalton (1982) have described a similar sequence of bryophyte colonisation following felling and burning of *E. regnans* forests in Tasmania.

Pot experiments comparing burnt and unburnt peat showed that *E. obliqua* grew rapidly on burnt peat and then became chlorotic, probably due to nutrient imbalance or toxicity. Similar observations of chlorosis and poor growth have been made by Smith (1983) for *Acacia dealbata* growing on red burnt soils (derived from intense sustained log fires).

However, any nutrient imbalance of the burnt soil resulting from the peat fire did not prevent establishment of eucalypt seedlings, whose height at 3 years (5.0 m) equalled that of seedlings growing on unburnt peat in open areas, in the gully nearby. It is possible that increased light and a reduction of allelopathic factors in the soil, following burning of the peat, may have also contributed to the dense and rapid growth of eucalypt seedlings on the burnt peat. Once the seedlings on burnt peat (subsite F2) reached the 2.0 m water table (at 2–3 years), their growth appeared faster than that of seedlings on unburnt peat soil in the adjacent gully complex (subsite F1).

Though peat fires are relatively rare in mainland Australia (Gill 1981), the present study indicates that they may cause significant changes in vegetation structure and floristics in some gully communities. In the present study, no resilience was shown by an *E. obliqua/ P. lasianthos/C. australis* gully community where a peat (ground) fire developed following a surface wildfire, as all the plants present at the time of the peat fire (including their buried seeds and propagules) were killed at or below ground level.

Similar lack of resilience has been reported following peat fires in *Melaleuca squarrosa* closed scrub on the humus-rich soil of the river valleys to the north and west of Anglesea with consequential changes in vegetation structure and floristics (Gill 1993; White 1994), and replacement of the *M. squarrosa* closed scrub by a *Eucalyptus aromaphloia* woodland.

The present study indicates that, in Victoria, peat fires may occasionally cause significant changes in vegetation structure and floristics. Management strategies are required to prevent and control in-ground fires, especially when they establish in communities of ecological significance (Gill 1993, 1994).

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REFERENCES

Andersen, A., 1987. A survey of the invertebrates of the Anglesea region following wildfire. Report to Angair Inc. 28 p. (unpublished).

Ashton, D. H., 1981. Fire in tall open-forests. In *Fire and the Australian Biota*, A. M. Gill, R. H. Groves & I. R. Noble, eds, Australian Academy of Science, Canberra, 341–366.

Ashton, D. H., 1986. Viability of seeds of *Eucalyptus obliqua* and *Leptospermum juniperinum* from capsules subjected to crown fire. *Australian Forestry* 49: 28–35.

Ashton, D. H. & Attiwill, P. M., 1994. Tall open-forests. In *Australian Vegetation*, R. H. Groves, ed., 2nd edition, Cambridge University Press, 157–196.

Ashton, D. H. & Frankenberg, J., 1976. Ecological studies of *Acmena smithii* (Poir) Merrill & Perry with special reference to Wilsons Promontory. *Australian Journal of Botany* 24: 453–487.

Auld, A. D. & O'Connell, M. A., 1991. Predicting patterns of post-fire germination in 35 eastern Australian Fabaceae. *Australian Journal of Ecology* 16: 53–70.

Backhouse, G. & Jeanes, J., 1995. *The Orchids of Victoria*. Melbourne University Press, Melbourne, 388 p.

Barnett, J. M., 1984. Initial effects of fire on orchids in a stringy-box forest. *Victorian Naturalist* 101: 188–190.

Chesterfield, E. A., Taylor, S. J. & Molnar, C. D., 1991. Recovery after wildfire: warm temperate rainforest at Jones Creek, East Gippsland, Victoria. *Australian Forestry* 54: 157–173.

Christensen, P. & Kimber, P., 1975. Effects of prescribed burning on the flora and fauna of south-west Australian forests. *Proceedings of the Ecological Society of Australia* 9: 85–107.

Christensen, P., Recher, H. & Hoare, J., 1981. Responses of open forests (dry sclerophyll forests) to fire regimes. In *Fire and the Australian Biota*, A. M. Gill, R. H. Groves & I. R. Noble, eds, Australian Academy of Science, Canberra, 367–394.

Coaldrake, J. E., 1961. Ecosystems of the coastal lowlands ('Wallum') southern Queensland. *CSIRO Australia Bulletin* No. 283, Melbourne, 1 map, 10 pls, 138 p.

Conole, L. & Baverstock, G., 1984. Birds of the western section of the Angahook-Lorne Forest Park, Victoria. *Geelong Naturalist* 21: 55–66.

Cremer, K. W. & Mount, A. B., 1965. Early stages of succession following complete felling and burning of a *Eucalyptus regnans* forest in the Florentine Valley, Tasmania. *Australian Journal of Botany* 13: 303–322.

Duncan, D. & Dalton, P. J., 1982. Recolonisation by bryophytes following fire. *Journal of Bryology* 12: 53–63.

Egler, F. E., 1954. Vegetation science concepts. I. Initial floristic composition, a factor in old field vegetation development. *Vegetatio* 4: 412–417.

Filson, R. B. & Rogers, R. W., 1976. *Lichens of South Australia*. South Australian Government Printer, Adelaide, 16 pls, 197 p.

Gill, A. M., 1975. Fire and the Australian flora: a review. *Australian Forestry* 38: 1–25.

Gill, A. M., 1981. Adaptive responses of Australian vascular plant species of fires. In *Fire and the Australian Biota*, A. M. Gill, R. H. Groves & I. R. Noble, eds, Australian Academy of Science, Canberra, 243–272.

Gill, A. M., 1993. Interplay of Victoria's flora with fire. In *Flora of Victoria*, Vol. I, *Introduction*, D. B. Foreman & N. G. Walsh, eds, Royal Botanic Gardens and National Herbarium, South Yarra, Victoria, 212–226.

Gill, A. M., 1994. How fires affect biodiversity. In

Fire and Biodiversity: Effects and Effectiveness of Fire Management, Biodiversity Series, Paper No. 8, Biodiversity Unit, Commonwealth of Australia, Department of Environment, Sport & Territories, Canberra, 47–55.

GILL, A. M. & BRADSTOCK, R., 1995. Extinction of biota by fires. In *Conserving Biodiversity: Threats and Solutions*, R. A. Bradstock, T. D. Auld, D. A. Keith, R. T. Kingsford, D. Lunney & P. D. Siversten, eds, Surrey Beatty & Sons, Sydney, 309–322.

GILL, A. M., MOORE, P. H. R. & MARTIN, W. K., 1994. *Bibliography of Fire Ecology in Australia (including Fire Science & Fire Management)*, Edition 4, NSW National Parks & Wildlife Service, Hurstville, New South Wales, 192 p.

HILL, R. S. & READ, J., 1984. Post-fire regeneration of rainforest and mixed forest in Western Tasmania. *Australian Journal of Botany* 32: 481–493.

LEITCH, C. J., FLINN, D. W., & VAN DE GRAAFF, R. H. M., 1983. Erosion and nutrient loss resulting from Ash Wednesday (Feb. 1983) wildfires: a case study. *Australian Forestry* 46: 173–180.

MAY, T. & FUHRER, B., 1989. Notes on fungi occurring after fire in Australia. 1. Introduction and description of *Gerronema postii*. *Victorian Naturalist* 106: 133–137.

PARSONS, R. F., KIRKPATRICK, J. B. & CARR, G. W., 1977. Native vegetation of the Otway region. *Proceedings of the Royal Society of Victoria* 89: 77–88.

PATE, J. S. & DIXON, K. W., 1982. Reserve substances of storage organs. In *Tuberous, Cormous and Bulbous Plants—Biology of an Adaptive Strategy in Western Australia*, J. S. Pate & K. W. Dixon, eds, University of Western Australia Press, Perth, 182–223.

PITT, A., 1977. Soils of the Otway Ranges and surrounding coastal plain. *Proceedings of the Royal Society of Victoria* 89: 69–75.

PITT, A. J., 1981. *A Study of the Land in the Catchments of the Otway Range and Adjacent Plains*. TC No. 14, Soil Conservation Authority, Kew, Victoria, 168 p.

PURDIE, R. W., 1977a. Early stages of regeneration after burning in dry sclerophyll vegetation. 1. Regeneration of the understorey by vegetative means. *Australian Journal of Botany* 25: 21–34.

PURDIE, R. W., 1977b. Early stages of regeneration after burning in dry sclerophyll vegetation. 2. Regeneration by seed germination. *Australian Journal of Botany* 25: 25–46.

PURDIE, R. W. & SLATYER, R. O., 1976. Vegetation succession after fire in sclerophyll woodland communities in south-eastern Australia. *Australian Journal of Ecology* 1: 223–236.

RAWSON, R. P., BILLING, P. R. & DAWSON, S. F., 1983. The 1982–83 forest fires in Victoria. *Australian Forestry* 46: 163–172.

REILLY, P., 1985. Victorian Group—Regeneration survey. *Royal Australasian Ornithologists Union Newsletter*, No. 64, p. 8.

REILLY, P., 1991a. Effect of wildfire on bird populations in a Victorian coastal habitat. *Emu* 91: 100–106.

REILLY, P., 1991b. The effect of wildfire on bush bird populations in six Victorian coastal habitats. *Corella* 15: 134–142.

ROSS, J. H. (ed.), 1993. *A Census of the Vascular Plants of Victoria*, 4th edition, National Herbarium of Victoria, South Yarra, plus update bulletins 4.1, 4.2, 4.3, 213 p.

ROSS, J. H. (ed), 1996. *A Census of the Vascular Plants of Victoria*, 5th edition, National Herbarium of Victoria, South Yarra, 230 p.

SCOTT, G. A. M., 1985. *Southern Australian Liverworts*. Aust. Flora & Fauna Series No. 2. Bureau of Flora & Fauna, Australian Government Publishing Service, Canberra, 216 p.

SCOTT, G. A. M. & STONE, I. G., 1976. *The Mosses of Southern Australia*. Academic Press, London, 495 p.

SMITH, D. J., 1983. Study on nitrogen fixation (acetylene reduction) in *Acacia dealbata* Link. BSc(hon) thesis. Botany School, University of Melbourne (unpublished).

SOUTHORN, A. L. D., 1977. Bryophyte colonisation of burnt ground with particular reference to *Funaria hygrometrica*. *Journal of Bryology* 9: 361–373.

SPECHT, R. L., 1970. Vegetation. In *The Australian Environment*, G. W. Leeper, ed., 4th Edition, CSIRO, Melbourne, 44–67.

SPECHT, R. L. & SPECHT, A., 1989. Species richness of sclerophyll (heathy) plant communities in Australia—the influence of overstorey cover. *Australian Journal of Botany* 37: 337–350.

WARK, M. C., 1996. Regeneration of heath and heath woodland in the north-eastern Otway ranges three to ten years after the wildfire of February 1983. *Proceedings of the Royal Society of Victoria* 108: 121–142.

WARK, M. C., WHITE, M. D., ROBERTSON, D. J. & MARRIOT, P. F., 1987. Regeneration of heath and heath woodland in the north-eastern Otway ranges following the wildfire of February 1983. *Proceedings of the Royal Society of Victoria* 99: 51–88.

WHITE, M. D., 1982. Anglesea–Aireys Inlet native plant list. In *Anglesea—A Natural History Study*, 5th edition, Angair Inc., Anglesea, Victoria, 38 p. (unpublished).

WHITE, M. D., 1994. Fire and vegetation in the Anglesea district. Angair Inc., pamphlet.

WILSON, B. A. & MOLONEY, D. J., 1985a. Small mammals in the Anglesea–Aireys Inlet area of Southern Victoria—a post fire study. *Victorian Naturalist* 102: 65–70.

WILSON, B. A. & MOLONEY, D. J., 1985b. An investigation of small mammal recolonisation and vegetation regeneration in fire affected areas of the Anglesea–Aireys Inlet region. Report to the Ministry of Conservation, Forests & Lands, Victoria, 40 p. (unpublished).

	Authority	
	Ross (1993)	Ross (1996)
Grasses	*Danthonia pallida*	*Joycea pallida*
	Danthonia semiannularis	*Notodanthonia semiannularis*
	Stipa rudis	*Austrostipa rudis*
	Stipa semibarbata	*Austrostipa semibarbata*
Shrubs	*Hibbertia riparia*	*Hibbertia riparia*
	Hibbertia stricta	*Hibbertia riparia*

Appendix. Nomenclature of vascular plants—name changes since the second paper in this series.